VARIATION IN THE PERFOLIATE UVULARIAS*

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In New England and New York, where the two perfoliate species of *Uvularia* are found, little difficulty is encountered in distinguishing them. Although both species in that area vary somewhat, *U. perfoliata* is small and glabrous, while *U. grandiflora* is distinctly larger and its leaves are pubescent on the lower surface. However, southward along the western border of the distribution of *U. perfoliata*, the variation within both species becomes so marked that for occasional collections the accepted criteria for distinguishing them breaks down. In the perfoliate species of *Uvularia*, variants more or less difficult to classify are most commonly found along a line roughly extending from Rochester, New York, down the Appalachian Mountains through eastern Tennessee and into northeastern Alabama. For example, while the New England botanist could tell at a glance the species to which a plant from the Berkshires belonged, he would require a hand-lens for classifying them in eastern Tennessee, and even with this aid several plants from a given woodland would probably be termed "special problems."

In order to measure this perplexing variation and to analyze its cause, the present project was undertaken. Mass collections of plants of *Uvularia perfoliata* and *U. grandiflora* were obtained from several collaborators, as listed below,[1] and they were supplemented by further collections made during the course of the investigation. Individuals from these mass collections were measured, the measurements covering the following characters:

Pubescence
Length of longest internode
Number of leaves
Number of fruits
Leaf index (leaf width/leaf length)
Leaf length
Leaf width
Leaf shape
Length of first internode below branch
Length of second internode below branch
Length of third internode below branch
Length of first internode, fertile branch
Length of first internode, sterile branch
Ratio of first internode on fertile branch to first internode on sterile branch
Length of each additional internode, sterile branch
Length of each additional internode, fertile branch
Shape of fruit
Length of fruit pedicel
Number of hairs per square millimeter on lower leaf surface
Length of hairs on lower leaf surface

Wherever the nature of the material permitted, these measurements were treated statistically. The method of pictorialized scatter diagrams was chosen to analyze these data, since it permits several variables to be depicted on a single chart

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rather than two, as in ordinary scatter diagrams. The first five characters in the above list were finally adopted for the charted data.

Mature plants were used in all measurements. A plant was considered mature when it had ceased elongating and the terminal leaves were fully expanded. This occurs at some time after the fruit has developed to a point where its mature form is clearly recognizable, two to three weeks after the perianth has fallen off. Depending on the clone and the environment, this may be from late April to mid-June. The plants remain in a "measurable" state from this time until the first autumn frost, except for the fruits, which reach full size about two months after the perianth has fallen.

Since plants in flower have not reached maximum growth, floral characteristics do not appear in the above list, but some discussion of floral characteristics is given later in this paper.

General Characteristics of the Perfoliate Uvularias

The perfoliate species of *Uvularia* constitute a natural division of the genus, and consist of two species, *U. perfoliata* and *U. grandiflora*. These are plants with a short rhizome containing numerous fleshy appendages, an aerial stem bearing

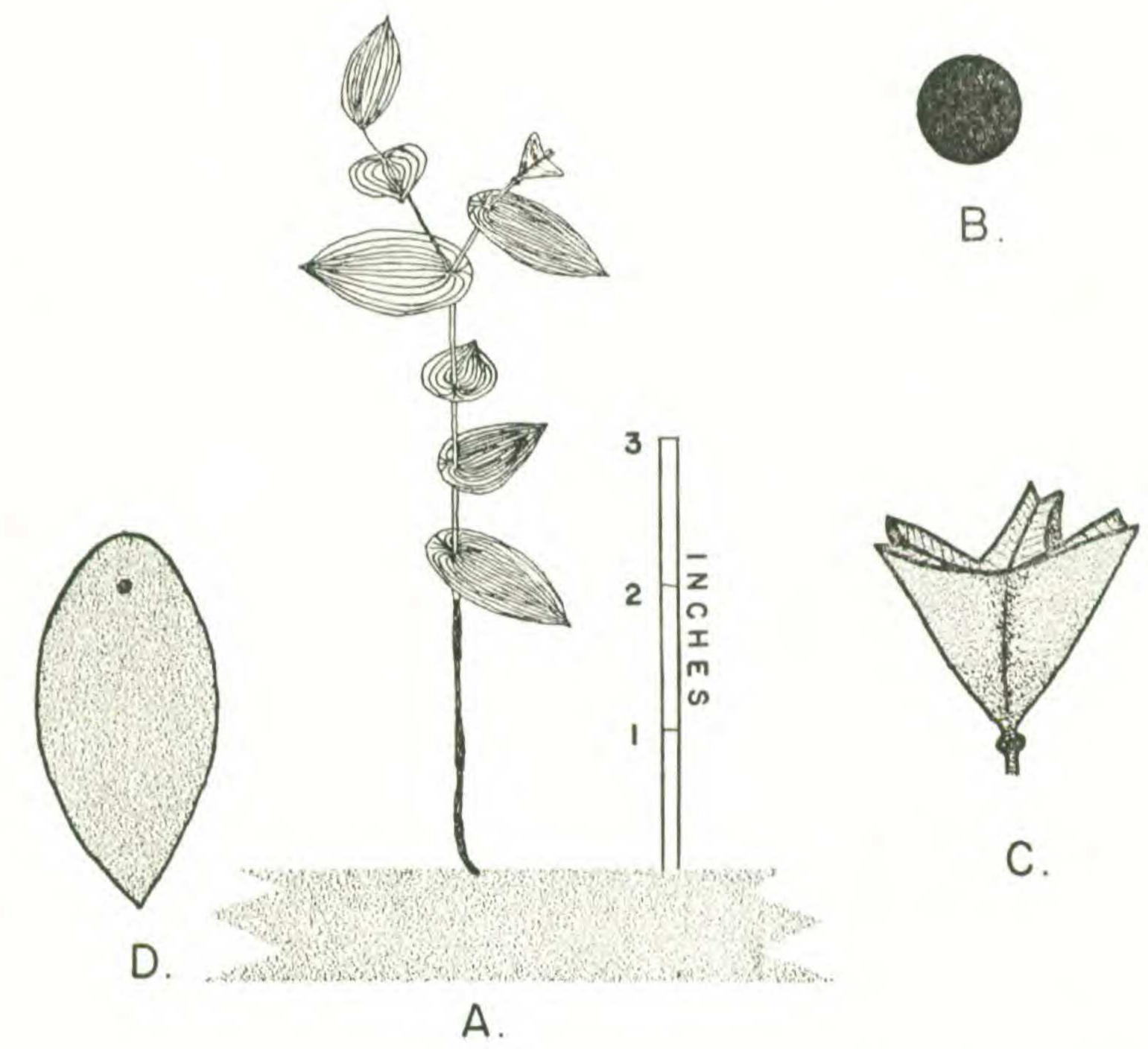


Fig. 1. *Uvularia perfoliata:* A, habit; B, dot as used on charts; C, fruit; D, leaf outline (× 2 habit scale).

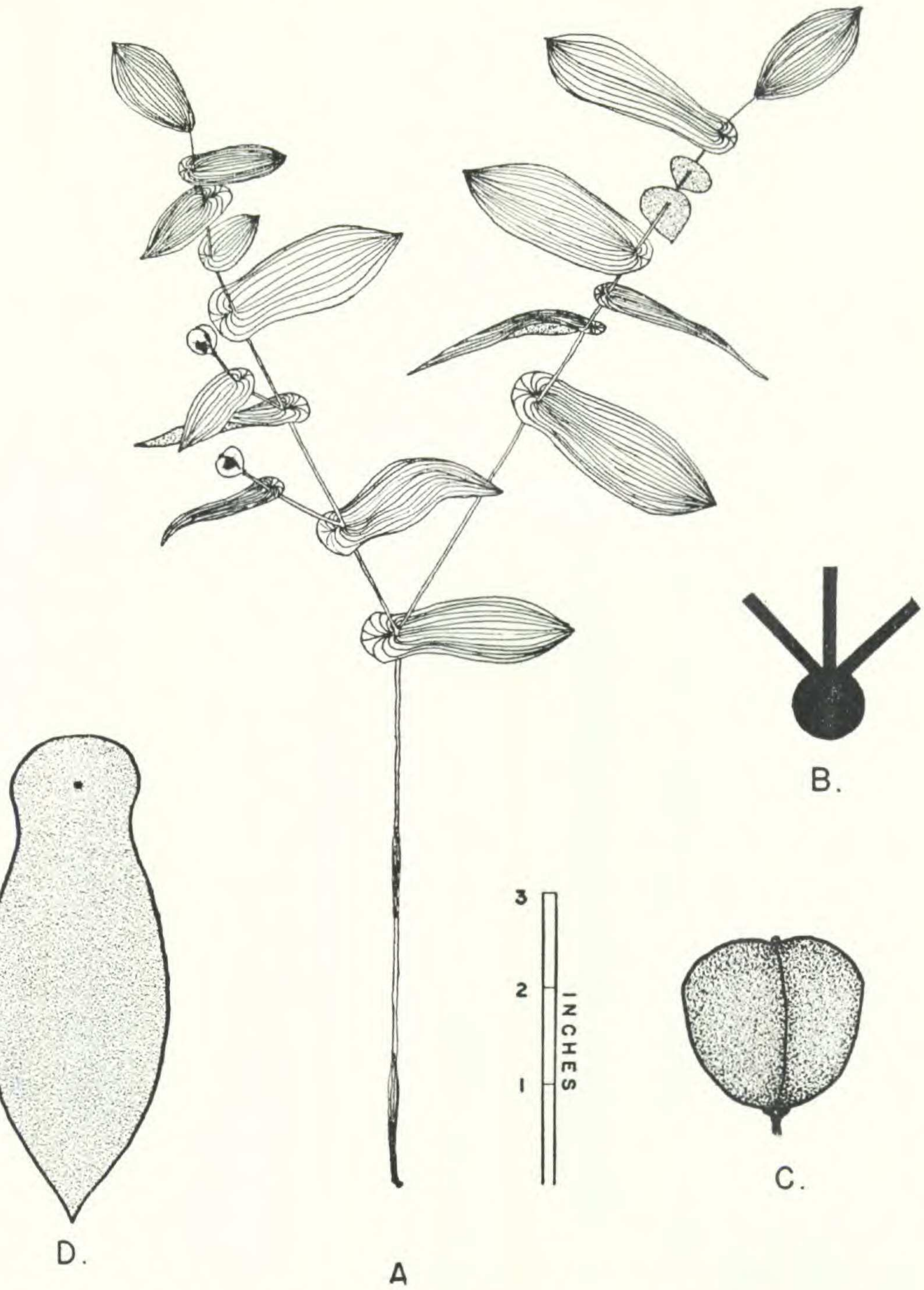
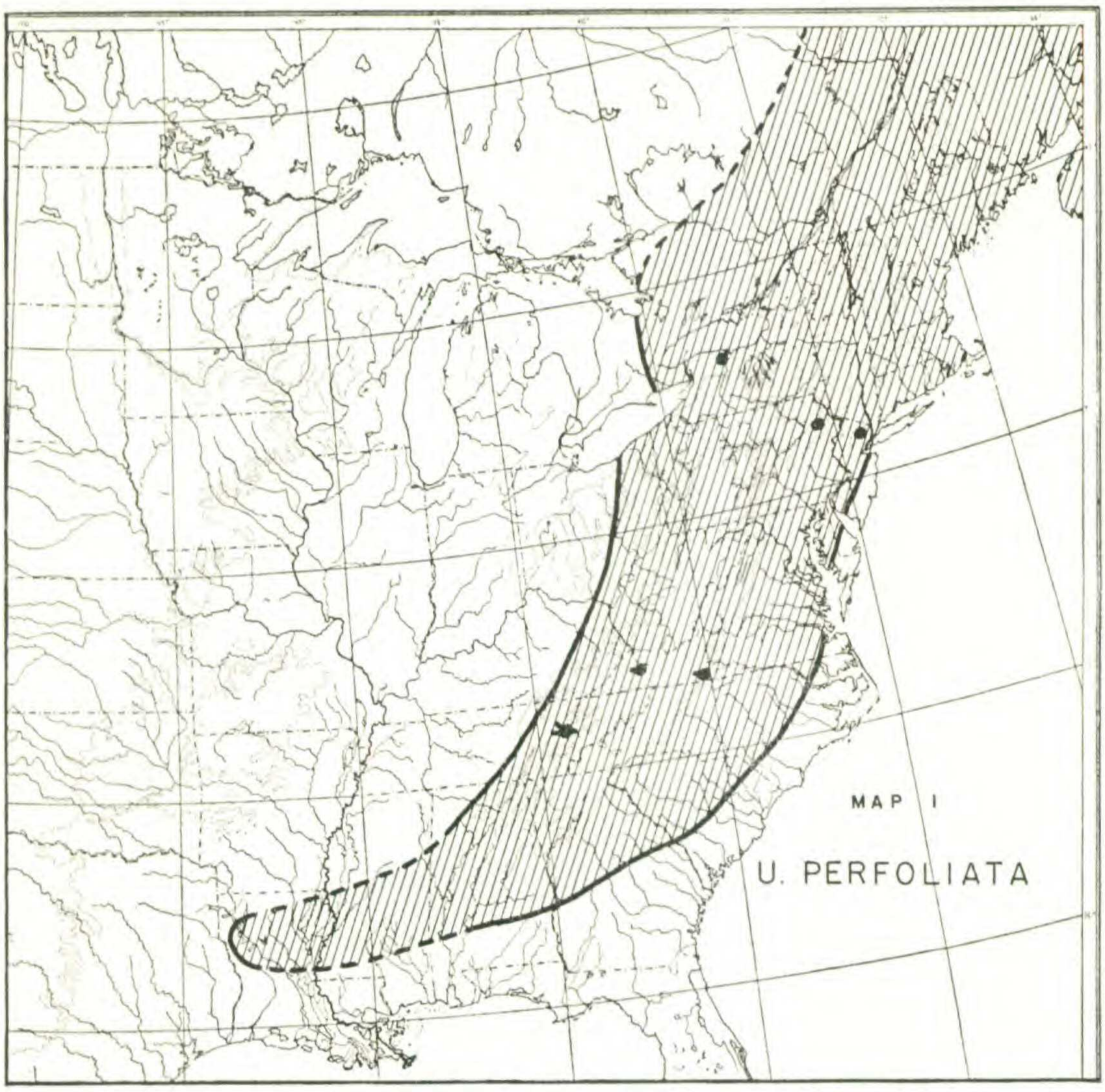


Fig. 2. *Uvularia grandiflora:* A, habit; B, dot as used on charts; C, fruit (about × 4 habit scale); D, leaf outline (×2 habit scale).

3–5 cataphylls below and 6–36 perfoliate leaves above. Mature plants characteristically are branched one or more times, the branching superficially resembling a true dichotomy. One to four flowers may be present on a given aerial stem. These are axillary, and are never borne below the lowest branch. The liliaceous perianth is made up of three yellow petals and three yellow sepals. The flowers droop, never developing the widely spreading perianth segments characteristic of such genera as *Lilium* or *Hyacinthus*. Flowering occurs within a few days to about



The symbols used on Maps 1 and 2 are similar to those on the charts. An additional pair of rays depicts the values found on the ordinate and abscissa, the ray to the left depicting the longest internode with increasing values to the left; that on the right, the leaf index with increasing values to the right.

a week after the first shoot appears above the ground and consequently before the plants have reached full size. Statistically useful data on vegetative parts of the plant are impossible at this stage. The 3-angled loculicidal fruit contains about 12 round, dark, hard seeds 2–3 mm. in diameter. The capsule shape varies from sharply acute at the tip to moderately obtuse and lobed (fig. 5).

Uvularia perfoliata and *U. grandiflora* are woodland plants, varying in their preference for deep or open situations, soil types, and plant associations. The plants usually persist from mid-spring to mid-autumn. Maximum growth on the aerial stems has occurred shortly after the fruits are large enough to be recognized. The plants used for measurements of vegetative parts in this project were all mature, in the sense that maximum growth had been reached.

Having considered the characteristics of the perfoliate Uvularias as a whole, the intraspecific characters will now be discussed.

Uvularia perfoliata.—This species was established in the first edition of Linnaeus' 'Species Plantarum,' in 1753. It is a small plant, with 5 to 8 leaves of which 3 or 4 are below its single branch. The leaves are glabrous, glaucous, oval and thin; the one subtending the branch is 65 mm. or less long. The longest stem internode, generally found below the lowest leaf, is 100 mm. or less long. The flower-bearing branch has a single leaf that subtends the flower. The single flower is pale yellow. The perianth segments have a granular appearance on the inside caused by rough, many-celled emergences. These are visible to the unaided eye, and under the hand lens are shown to be small papillae. The 6 stamens are as long or shorter than the trifid style. The tips of the anthers are pointed. The three-angled capsule of the fruit is broader than long (each angle two-ridged), the tip acute (fig. 1C).

Uvularia perfoliata is found in rather open woods, in neutral or slightly acid soil, frequently under white oaks and rarely under red oaks. Our collecting experience has been that the species was never particularly abundant in the mature form. Seedlings and sexually immature, non-branching older plants are not uncommon in many white oak woods, but these are nearly useless for comparative purposes.

Uvularia grandiflora.—James E. Smith, the British botanist, described this species in his 'Exotic Botany' in 1804. It is a considerably larger plant than *U. perfoliata,* sometimes waist-high. There is a single leaf below the lowest branch. Generally there are 16 or more leaves on the plant, and there may be as many as 36. These are pubescent below, dark green, thicker than those of *U. perfoliata* and frequently shaped like a "Dutchman's shoe" (fig. 2D). The leaf subtending the branch is 85 mm. or more long, typically 100–130 mm. long. The longest stem internode, generally found below the lowest leaf, is 150 mm. or longer. Flowers may be borne on either the main branch, or on secondary or tertiary side branches, and generally number from 1 to 4. The branches are leafy. The flowers are yellow, somewhat brighter than those of *U. perfoliata.* The perianth segments are smooth on the inside. The 6 stamens are longer than the style, with blunt-tipped anthers. The three-angled capsule of the fruit is obtusely lobed at the tip (fig. 2C).

Uvularia grandiflora usually grows in deep woods, in beech-maple forests or in oak-hickory forests, and there is no apparent preference for red or white oaks. It is generally found abundantly in mature stages. One clone in Michigan, measuring about 5 × 8 feet, contained more than 50 mature aerial stems. On a southern Wisconsin hillside collecting 25 plants made no visible reduction in the apparent abundance.

The following table summarizes the distinctions between *Uvularia perfoliata* and *U. grandiflora.* Because of the high degree of intermediacy along the zone of overlap of the two species, it is more practical to list those characters least like those of the other species. It is intended that the assumption should hold, viz., that the perfoliate *Uvularia* least like *grandiflora* is, in nature, the best *Uvularia perfoliata,* and also the converse must be true.

A COMPARISON OF THE PERFOLIATE UVULARIAS

Uvularia perfoliata (least like *U. grandiflora*)	*Uvularia grandiflora* (least like *U. perfoliata*)
Flower	
Solitary	1–4
Perianth granular-rough within	Perianth smooth within
Stamens equal in length to style or shorter	Stamens longer than style
Anthers pointed at tip	Anthers blunt-tipped
Fruit	
Capsule acutely truncate	Capsules obtusely lobed
Leaves	
Lower surface glabrous	Lower surface strongly pubescent
3 or 4 below lowest branch	One below lowest branch
Branch-subtending leaf 65 mm. or less long	Branch-subtending leaf 85 mm. or more long
5–8 per plant	13–36 per plant
Fertile branch with one leaf	Fertile branch with many leaves
Glaucous	Deep green
Smooth, thin	Rough, thick
Oval	Mature leaves shaped like a "Dutchman's shoe"
Size	
Longest internode 100 mm. or less	Longest internode 150 mm. or more

History of the Perfoliate Uvularias

The perfoliate species of *Uvularia* are sufficiently distinct from other Liliaceae to make their botanical position clear, and, with perhaps one exception, the history of this group does not show that these plants were ever confused with those of closely allied genera. What confusion has existed lies between inter-specific, rather than inter-generic, similarities.

As indicated in the preceding section, *Uvularia perfoliata* is a Linnean species and *U. grandiflora* was established by Smith in 1804. At the same time that Smith established *U. grandiflora,* he described another species from eastern America which he named *Uvularia flava.* Described as rare, *U. flava* was similar to *U. perfoliata* but with deeper yellow flowers and perianth smooth within—floral characteristics which suggest *U. grandiflora. U. flava* was recorded from New Jersey to Virginia, well within the range of *U. perfoliata,* and on the extreme eastern boundary of the distribution of *U. grandiflora. U. flava* appears to have been a hybrid between *U. perfoliata* and *U. grandiflora* and is no longer recognized as a species.

Fig. 3. Knoxville "Collection A"

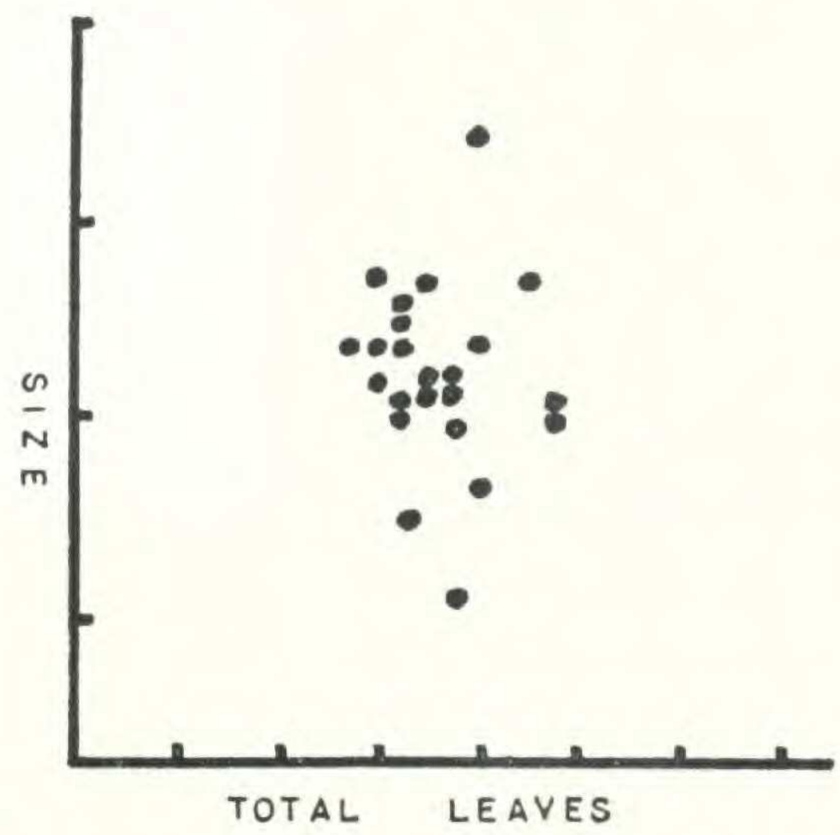


Fig. 4. Knoxville "Collection B"

These scatter diagrams show the size (length of longest internode) plotted against the total number of leaves on the plant. Note the high degree of overlap between the two collections.

Walter's collection of American plants, made in the latter half of the eighteenth century, contained a plant which he called *Anonymos (Erythronio affinis) pudica.* Walter did not collect or identify as such any plants of *Uvularia,* but from the description (Fl. Carol. 1788) his plant undoubtedly refers to a species of that genus. Michaux (Fl. Bor. Am. 1803) considered Walter's specimen to be *U. perfoliata.* In 1833 Asa Gray noted that it resembled the mountain *Uvularia, U. puberula* Michx. Unfortunately, the specimen now appears to be lost; at least it is not in the British Museum where Walter's herbarium is kept. We today have only Walter's description to show what the plant may have been. This reads, in part: "capsula turbinato-triangularis, angulis bifidis, trilocularis, trivalvis," and "foliis amplexicaulibus."

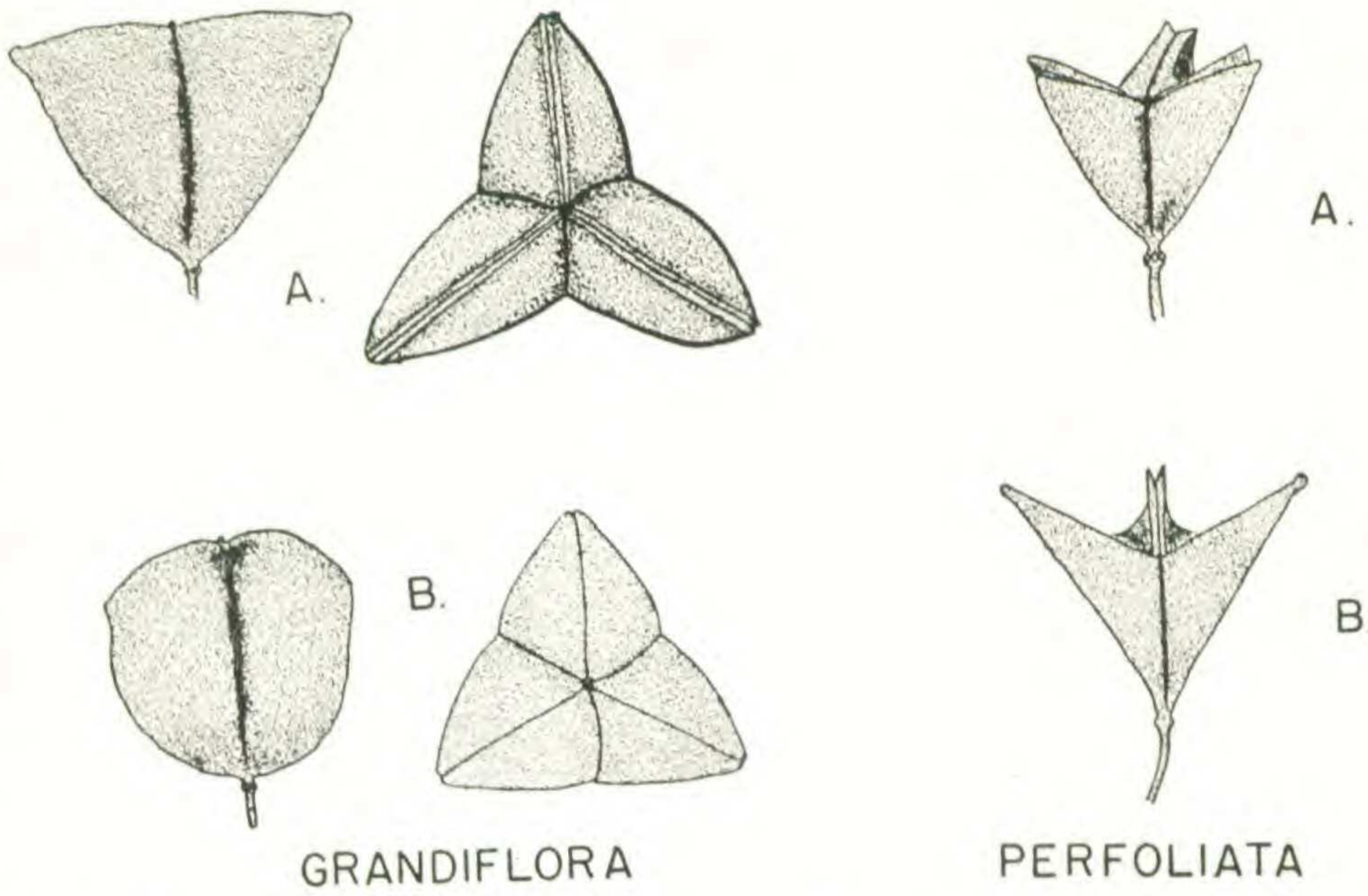


Fig. 5. Capsule types: Left—A and B, Billington; Right—A, Ridgewood; B, Monte Sano.

Fernald (Gray's Manual, 1939) uses this plant of Walter's to establish *Uvularia pudica* (= *Uvularia puberula* Michx.). *U. puberula* is a sessile-leaved plant, and the leaves are not "amplexicaul," although for a few days after the shoot of this plant appears above the ground the leaves *appear* to clasp the stem, due to their folding within the bud. Depending upon the interpretation, the capsules of either *U. puberula* or *U. perfoliata* might be considered "top-shaped." It may be that Walter's plant was a perfoliate *Uvularia*, as Michaux suggested, and not a sessile-leaved form. In any case, it appears that the name *Uvularia pudica* should be discarded and Michaux's *U. puberula* restored.

Nuttall recognized a distinction between the eastern and western populations of the perfoliate Uvularias, apparently without having read Smith's description of *U. grandiflora*. He wrote in his diary on May 14, 1810, in northwestern Pennsylvania, "There is in these swamps also abundance of a plant which I at 1st took to be *Uvularia perfoliata*, but it is much larger than I have usually seen it, the style is trifid nearly to its base; the filaments are very thick subulate & alternately longer."

The various manuals of the flora of eastern North America give the following references to perfoliate species of Uvularia:

Eaton, Amos, *Manual of Botany for North America*. 1833. Eaton notes that *Uvularia flava* equals *Anonymos pudica* Wr., and asks, "Is this distinct from the preceding [*perfoliata*]?"

Wood, Alphonso, *Flora and Class-Book*. 1846. Two species recognized, *grandiflora* and *perfoliata*. Wood notes that *flava* equals *perfoliata*.

Gray, Asa, *Manual of Botany*. 1857. Two species, *grandiflora* and *perfoliata*.

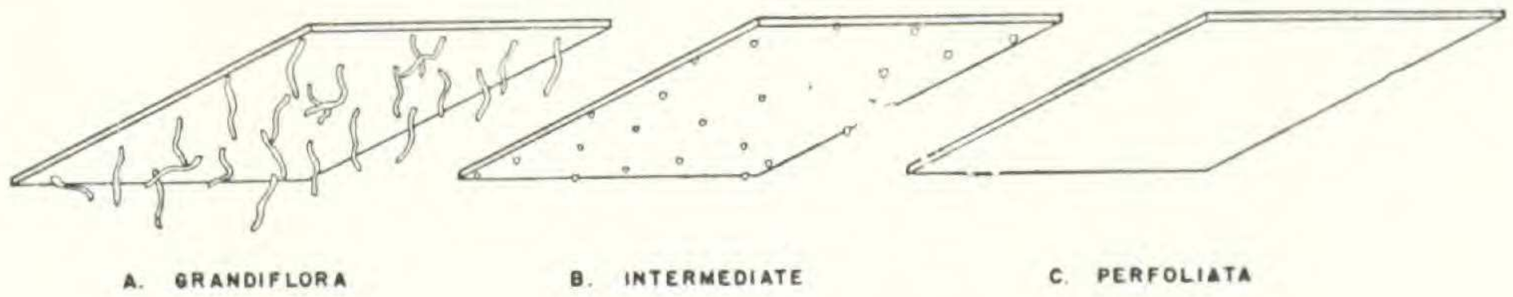


Fig. 6. Vesture types.

Gray, Asa, *Manual of Botany.* 1868. As above, with *flava* added as a distinct species.

Gray, Asa, *Manual of Botany.* 1887. The species name *flava* is dropped and never reappears in our floras.

The variation within the perfoliate Uvularias led Anderson and Whitaker to look for gross genetic differences in the chromosomes of the two species. They found (1934) that the chromosomes were so similar that the variation could not be ascribed to any gross genetic differences. In a short note, Anderson and Hubricht (1943) pointed out that the difference in leaf texture between *U. perfoliata* and *U. grandiflora* could be attributed to cellular differences in the epidermis.

From this brief history of the genus it may be seen that the problems in identification of the perfoliate Uvularias are *U. flava* and Walter's *Anonymos pudica. U. flava* may be attributed to hybridization and *Anonymos pudica* may belong with the perfoliate Uvularias rather than with Michaux's *U. puberula.* The body of this paper, then, will deal solely with the observed variations between *U. perfoliata* and *U. grandiflora,* and an interpretation of these varieties.

Analysis of Variation in the Perfoliate Uvularias

During the course of this investigation, thirty-four collections of population samples from seventeen states and one Canadian province were examined and measured. These mostly represented small collections of one to twelve specimens from any single locality. In fourteen cases, more than a dozen specimens from one locality were available. The data for each collection were transferred to a pictorialized scatter diagram to show the extent of the variation in that population. For example, in Monroe County, New York, four collections were made, three of which contained from six to twelve specimens, the fourth, thirty-five. In each the variation was measured and treated statistically, but only in the fourth collection (Oakwood Park) were the data placed in a pictorialized scatter diagram. As a result, the diagrams reproduced in this paper represent only a portion of the specimens examined and measured, but because they picture those populations from which the largest number of plants was taken, they are perhaps most valuable for determining the extent of variation in the perfoliate species of *Uvularia.*

The Pictorialized Scatter Diagram.—This technique was developed by Anderson and his students (see Anderson, 1948; Hall, 1952; Sauer, 1951) in their studies

on variation. It has an advantage over conventional scatter diagrams or graphs in that more than two characters (in this case five) may be plotted on a given set of coordinates. For diagrams in this paper, the length of the longest internode (a measure of the plant's height) is plotted on the ordinate, and the leaf index (ratio of leaf width to length; shape) on the abscissa. For a given specimen, a dot corresponding to the length of its longest internode plotted against its leaf index is placed on the chart, as in conventional scatter diagrams. From this dot, rays emanate in various positions and of varying lengths to denote other character measurements. Figure 2B illustrates this construction as applied to *U. grandiflora.* There are three rays. The center one, which stands straight up, represents the number of fruits on the plant. Where there is only 1 fruit, the ray is absent; where there are 2–4, the ray is drawn full length. The ray angling out to the left of the central one denotes the total number of leaves on the plant. Where there are 9 or less leaves, this ray is absent; where there are 10–12, the ray is very short; 13–15 leaves brings the ray out to half-length, and 16–36 leaves are marked by a full-length ray. The third ray, angling off to the right of the central arm, denotes pubescence on the lower leaf surface. An absence of this ray indicates no hairs; intermediate pubescence is shown by a line of half length; and full pubescence is shown by a full-length ray.

Charts 1 and 2 were made from herbarium specimens in the Missouri Botanical Garden. Chart 1 shows *Uvularia perfoliata,* and chart 2, *U. grandiflora.* The herbarium contains more than 200 specimens of perfoliate species of *Uvularia,* but most of these could not be measured either because they were flowering and therefore not fully grown, or they were fragmentary, or they were seedlings. All measurable plants were placed on the charts.

Uvularia perfoliata falls largely in the lower left-hand corner, and consists of dots with no arms or very short arms. The three aberrant examples with one or more long arms in chart 1 are special cases. They are all located in the southern part of the range (southern Virginia, Georgia, and Alabama) where variation in this species tends to be greater, as will be shown below. *Uvularia grandiflora,* on the other hand, tends to occur in the upper right-hand corner of the chart, and the dots are generally long-rayed.

These charts, then, reveal what is already well-known, that is, that *Uvularia perfoliata* is in general a small plant, has few leaves which are wide with respect to their length, a single fruit, and no pubescence. *Uvularia grandiflora* is larger, has many leaves which are narrower with respect to their length, more than one fruit, and is pubescent on the lower surface of the leaf. The distinctions are usually clear, indicating that the two are "good" species.

Preliminary examination of the perfoliate Uvularias, however, showed that a few populations were so intermediate that their identification was made only with difficulty, and when made it might still be open to some question. Shifting measured characters from the ordinate to the abscissa to the rays of the dots, as

well as using other characters than the five finally adopted, were tried before the final form of the charts was decided upon. This final form is an attempt to stress significant differences, in order to separate the species as far as possible, both in their position on the chart and in the number and length of the rays on the dots. As an example of this, when a collection of *U. perfoliata* and of *U. grandiflora* from two different locations near Knoxville, Tenn. were first examined, their similarity, except for pubescence, was most marked. One experiment in chart construction plotted the length of the longest internode on the ordinate against the total number of leaves on the abscissa. So plotted, the charts of each population almost exactly coincided spatially (figs. 3, 4). In the final chart form adopted, there is greater separation (charts 8, 9).

Keeping in mind the intermediacy of some collections, plants whose position on the chart fell in the lower left-hand corner and which consisted of dots with few or no rays, were considered as being less like *grandiflora* rather than more like *perfoliata*. In practice, these mean much the same thing, but in designating specimens as "less like *grandiflora*" or "less like *perfoliata*," depending on whether they fell in the lower left corner and had no rays or in the upper right corner and had long rays, we avoid the danger of setting up arbitrary standards for a species which might conceivably be at variance with the standards set up by the original describer for his type specimen. A "type" may, after all, not be "typical" of the species, yet taxonomically we cannot ignore the standards established by it on this account alone. Therefore, in analyzing the charts, we shall start with those populations least like *grandiflora* and conclude with those least like *perfoliata*.

Ridgewood, N. J. (Chart 3).—This locality is about the center of the range of *U. perfoliata*. The plants collected had invaded a rock garden in an essentially little disturbed residential area which was once a beech woods. They were not planted there, and the owner was ignorant of their presence. It might be observed that they were found in the course of a collecting trip which eventually covered over 4,000 miles, and, oddly enough, they were less than 30 feet from the kitchen door of the home of the writer's parents, a pleasant surprise to him on the halfway spot in an often discouraging trip.

All but three plants from this population were small, had 9 or less oval leaves, a single fruit, and no pubescence. The population was, in fact, less like *U. grandiflora* than any other charted. Three plants had 10 leaves, exhibiting to a very slight degree the leafiness characteristic of *grandiflora*. One plant had 2 fruits—quite unusual for *perfoliata*. In the sense that they were least like *U. grandiflora*, the Ridgewood population was the "best" *U. perfoliata* obtained in the mass collections. There is no indication that the variation is due to anything other than environment and normal heredity.

Hawley, Pa. (Chart 4).—Like the Ridgewood population, less than 100 miles away, this eastern Pennsylvania collection is in the middle of the range of *U. perfoliata*. The forest in which they were found contained areas of white oak predominance and areas of red oak predominance. The plants were found only in

the white-oak areas. There were about half a dozen sterile plants and seedlings for every fruiting plant, unlike Ridgewood where 16 of 23 plants were in fruit. The population is more variable than the preceding one with respect to leaf shape and height, but only one specimen had more than 9 leaves (it had 11) and none had more than one fruit.

In the same forest at the same time, but some distance from the previous population, in a ravine and near a creek, *Uvularia sessilifolia* was collected. The plants of *U. perfoliata* from Hawley do not show any indication of ever having formed hybrids with that species. There is some evidence that a *U. grandiflora* × *U. sessilifolia* cross has been successful in nature (see Red Lake, Minnesota), and that a *perfoliata* × *grandiflora* × *puberula* cross (the latter a sessile-leaved *Uvularia*) has occurred in Alabama (see below). It is, therefore, noteworthy that a *Uvularia* cross apparently did not occur at Hawley where two species occur together.

The high incidence of sterile (*i.e.*, non-flowering) plants in proportion to the fruiting ones was not uncommon in the collections of *perfoliata* made during this study. Plants of *U. perfoliata* were usually found spread out over a rather wide area, and only a small percentage of them were fruiting. *U. grandiflora*, on the other hand, was usually growing in tight colonies, with nearly all the plants fruiting (see Billington Woods, Mich.).

Dyestone Creek, Va. (Chart 5).—These plants were collected along the base of Smith Mountain, Pittsylvania County, on the southern border of Virginia. They are larger plants than those preceding. Nine plants (25 per cent) have more than 9 leaves; six plants (17 per cent) have the longest internode more than 100 mm. long; and one plant has 13 leaves and 3 fruits. The plant with 3 fruits and 13 leaves looks very much like a *U. grandiflora* except for its lack of pubescence.

Mountain Lake, Va. (Chart 6).—This population was located in Giles County, about 100 miles west of the Dyestone Creek population, on the grounds of the University of Virginia Mountain Lake Biological Station. An elevation of about 4000 feet makes the climate more like that in the more northern areas of *U. perfoliata* distribution, although the summer day length is, naturally, somewhat shorter. The collection was made east of the camp site. *U. perfoliata* was growing interspersed with *U. puberula*. For *U. perfoliata*, these were unusually tall plants, eight plants (61 per cent) being found with the longest internode more than 100 mm. Six plants (46 per cent) had 10 or more leaves.

Oakwood Park, N. Y. (Chart 7).—Located in Monroe County, on the east side of Irondequoit Bay, north of Rochester, Oakwood Park (apparently the name of a real-estate development) is near the western boundary of the range of *U. perfoliata*. Although the plants found here are small, like most of that species, the leaves are narrower than usual with respect to their length. Nineteen plants (54 per cent) exhibit a curious intermediate pubescence on the lower surface of the leaves (fig. 6B). Eight plants (23 per cent) have 10–12 leaves. The same intermediate

pubescence is found in two smaller *U. perfoliata* populations collected in Rochester. In the southwest portion of Monroe County a population containing both *U. perfoliata* and *U. grandiflora* was collected. *U. grandiflora* is reputed to grow around the shores of Irondequoit Bay, although none was found during a brief visit in 1951.

In many respects the Oakwood Park collection represents a high degree of intermediacy between *U. perfoliata* and *U. grandiflora.* This point is elaborated in the discussion following the presentation of charted data.

Knoxville, Tenn., Collection "A" (Chart 8).—A population was collected from the University of Tennessee farm woodlot about one mile south of the University campus, by R. E. Shanks. He described the situation as an open canopy with a heavy ground cover dominated by *Rhus, Laportea,* and *Galium.* This population will be discussed in conjunction with the following one.

Knoxville, Tenn., Collection "B" (Chart 9).—This sample was collected on the same day as the preceding one by Dr. Shanks from a wooded slope on the University farm. It was found under a heavy canopy of mixed deciduous trees, in a ground cover rich with *Trillium, Hepatica, Disporum, Polygonatum, Smilacina,* and *Viola.*

These populations represent our best mass-collection data on the perplexing problem of intermediacy. From a casual inspection, the plants from both collections appear to be *Uvularia grandiflora.* Closer inspection reveals that collection "A" consists of plants with leaves glabrous underneath. Still closer inspection shows that one plant of collection "A" possesses a single leaf with full-length hairs near the base on the underside. When this particular sample is under the binocular dissection microscope, the visible field is in no way different from that characteristic of *U. grandiflora,* although the rest of the leaves when viewed under the microscope are characteristic of *U. perfoliata.*

The label for collection "A" states that it is a population of *U. perfoliata,* while that for collection "B" states that it is a population of *U. grandiflora.* There is no question but that collection "B" consists of essentially *U. grandiflora* plants. However, when Chart 9 is compared with the charts which follow, the Knoxville *U. grandiflora* plants are found to be rather uniformly smaller than is typical for that species and are generally less heavily fruited. In addition, only six plants (19 per cent) have as many as 16 leaves, and five plants (16 per cent), have 12 or less. In short, the Knoxville *U. grandiflora* plants plot out on the chart as a group somewhat closer to typical *U. perfoliata* than any other group of *U. grandiflora.*

Collection "A" is a more questionable population. These plants exhibit characteristics of both species. As a group, they lean perhaps more toward *U. perfoliata* than toward *U. grandiflora.* The rather large size of the plants, and the leaf shape as reflected in the leaf indices, is more like *grandiflora* than *perfoliata.* Similarly, eight plants (40 per cent) have 13 or more leaves, and only six plants (30 per cent) have 9 or less leaves. The population is, therefore, leafier than is usual in

U. perfoliata. On the other hand, with the exception noted, the plants have the typical glabrosity of *U. perfoliata.* In another characteristic, not plotted on the chart, twenty plants (100 per cent) had 2 or more leaves below the primary branch, and seven of these (35 per cent) had 3 or more. This leafiness below the primary branch is characteristic of *U. perfoliata.* Collection "B" exhibited more of this characteristic than is usual in *U. grandiflora,* but not to the degree of collection "A."

Both Knoxville collections, then, represent intermediate plants. In collection "B" the taxonomic classification is not difficult; collection "A" is more of a problem. This area is used by classes of the University of Tennessee for ecological studies. It is a valley, rather wet at the bottom, with sloping hills delimiting it. Collection "A" was made on the bottom lands and collection "B" on the hillside, each in a distinct environment. Ordinarily one might expect to find *U. grandiflora* populations in moister locations than those of *U. perfoliata,* but the *grandiflora* populations were from the hillside of the campus and the *perfoliata* collection in the moister bottom area.

Debbink, Oconomowoc, Wisc. (Chart 10).—Near the shore of Lac La Belle, Oconomowoc, *Uvularia* was growing under an open canopy of *Tilia, Ulmus, Acer,* and among *Smilacina, Podophyllum, Pteris,* and *Equisetum.* Although clearly *U. grandiflora,* plants in this collection are smaller than usual for this species, and the leaf shape is quite variable. Only three plants (12 per cent) have more than one fruit. Ten plants (40 per cent) have less than 16 leaves, although one plant has 27. The leaf color of the fresh specimens was quite variable, ranging from deeply bluish-green, through dark green to yellowish-green.

La Barque Creek, Mo. (Chart 11).—Found in mixed woods at the base of a sandstone bluff in the La Barque Creek area south of Eureka, Missouri, this collection consists of moderately large plants with narrower leaves than usual for *U. grandiflora.* Notable in this population is the complete absence of plants with more than one fruit. *U. sessilifolia,* like *U. perfoliata,* is typically a single-fruited plant. It is found in Missouri, although more frequently north of the Missouri River than south of it.

Butts, Mo. (Chart 12).—Another small collection like the preceding was gathered from low woods near Courtois Creek. It is a little more typical of *U. grandiflora* than the La Barque Creek population. On only one plant is the longest internode less than 150 mm. Six plants (46 per cent) have 16 or more leaves; all plants have 14 or more leaves.

Red Lake, Minn. (Chart 13).—These plants from northern Minnesota are far removed from any juxtaposition with *U. perfoliata,* and, on the chart, they tend to congregate in the upper right hand corner, as should be expected for *U. grandiflora.* However, the fact that twenty-four plants in the population (96 per cent) lack three full-length rays on the dots used to plot them indicates that in some manner they fall short of being "good grandifloras." This point is discussed following the description of the charted data.

Clarksville, Mo. (Chart 14).—The Clarksville population was collected on the upper slopes of one of the characteristic glacial knobs of southern Pike County. The plants were growing under a heavy canopy of mixed deciduous trees, with *Bidens, Hystrix, Smilacina,* and *Polygonatum.* Although the leaf indices of this population are quite low, there are only three plants (11 per cent) whose longest internode is greater than 200 mm., and only two plants (8 per cent) which, on the basis of all five characters, are "good grandifloras." These two plants are in the upper right portion of the chart.

Coxsackie, N. Y. (Chart 15).—Coxsackie is in Greene County, on the Hudson River about 22 miles south of Albany. It is therefore well within the range of *U. perfoliata.* Six plants (31 per cent) are really "good grandifloras"; that is, they are tall, have a low leaf index and a complete set of full-length rays on the chart. These six plants are, in general, in the upper right portion of the chart. The smallest plants charted tend to have higher leaf indices and incomplete ray systems; in other words, the plants in the lower portion of the chart tend to be less *grandiflora*-like than the others.

Missouri (Chart 16).—This chart depicts a synthetic population. It was constructed from material in the Missouri Botanical Garden Herbarium which had been collected in Missouri. As a rule, there is only one plant from each county. Most of the plants were not mature and fruiting; the 35 plants which were measurable are included on the chart.

These plants plot out rather well for *U. grandiflora.* Fourteen plants (40 per cent) have complete sets of rays on the dots used to plot them. The "average plant" has the longest internode, 191.4 mm., a leaf index of .372, 16½ leaves, and 1½ fruits, and is fully pubescent. With the addition of half a fruit, this rather grotesque "average plant" would make an excellent *U. grandiflora.*

This general Missouri collection averages more like *grandiflora* than the individual Missouri collections. The explanation may lie in the fact that plant collectors usually strive to collect the best specimens for herbarium material, whereas a mass collection aims for a cross-section of the population.

Billington Woods, Institute Grounds, Bloomfield Hills, Mich. (Chart 17).—This *Uvularia* population, which appears to be a single clone, covered an area of about 5 × 8 feet, and contained well over fifty fruiting stems, crowded too closely together for exact counting. The plants were growing in a moderately open place in deep, moist woods. The adjacent trees were *Ulmus fulva, Carya tomentosa, C. ovata,* and *Cercis canadensis. Osmorhiza* grew around the edge of the clone.

This population was the least *perfoliata*-like of the mass collection material. There was a high percentage of secondary and even tertiary branching. Thirteen plants (72 per cent) had more than one fruit; the average was 2.5, as many plants had 3 fruits, and a few had 4. Other averages, which reveal the *grandiflora* characteristics of the population, are as follows: length of longest internode, 200.5 mm.; leaf index, .298; total leaves, 17; pubescence, complete in all specimens.

UNCHARTED COLLECTIONS

Some smaller collections, not charted, are nevertheless noteworthy, and are listed below:

Natchitoches, La.—In 1935 Anderson noted the existence of *U. perfoliata* in a woods along Grand Ecore Road, about two miles west of Natchitoches. Natchitoches is an extension of the previously known range of *U. perfoliata* by about 400 miles. These woods range from dry to wet enough for *Taxodium* with well-developed "knees." Occasional trees bearing *Tillandsia usneoides* provide an environment contrasting strongly with that of *U. perfoliata* in New England.

Five specimens, including Anderson's and several from the herbarium of the Northwest Louisiana State Teachers College, are available for study. All have at least three leaves below the single branch. All are small plants, with few leaves. Four are too early in the fruiting stage to get much of a picture of capsule shape, or more than a general picture of the ultimate measurements. This general picture suggests, however, that these plants are remarkably "good perfoliatas." The nearest plants of *Uvularia grandiflora* are some 250 miles to the north, in central Arkansas.[2]

Monte Sano, Ala.—One plant and several fragments from the herbarium of the New York State Museum came from rich woods, over limestone, near the summit of Monte Sano in Madison County. The size and shape of the leaf are as in *U. grandiflora.* All the leaves of the pressed specimens are so thin and translucent that newspaper sub-heads can be read clearly through them. Most of the leaves are completely glabrous, those which are not glabrous are very sparsely pubescent; where *U. grandiflora* will have well over 10 hairs per sq. mm., these plants have 1 hair to about every 5 sq. mm. The pubescent specimen in Knoxville "A" was completely pubescent, and the Oakwood Park specimens with intermediate pubescence had these emergencies with the same relative density as typical *U. grandiflora.* One of the fruiting specimens from Monte Sano contained a detached flower, which may or may not have belonged to it. The inner surface of the perianth segments of this flower was smooth, as in *U. grandiflora,* but there were about three places on each segment where rudimentary papillae could clearly be seen. The population sample is too small for the formulation of any definite conclusions.

If it be possible, an even more perplexing specimen—a single sheet in the Missouri Botanical Garden Herbarium (#1267594)—from Scottsboro, Alabama—possesses characters of *U. perfoliata, U. grandiflora,* and *U. puberula.* It has leaves slightly pubescent on the dorsal surface, an extreme *perfoliata* fruit, and angles of the stem are pubescent. Furthermore, although perfoliate, the form of the plant is more like *puberula* than either of the perfoliate species.

From these rather meager data, it appears as though the perfoliate Uvularias from northern Alabama are at least as variable as the Rochester or the Knoxville populations.

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[2] A collecting trip to Natchitoches in 1951 failed to augment these with mass-collection data.

An Interpretation of the Variation in the Perfoliate Uvularias

The concept of introgressive hybridization was developed by Anderson (Anderson and Hubricht, 1938; Anderson, 1949, 1950). Introgressive hybridization, or more simply, introgression, may be defined as the inherited variation in a species which results from back-crossing an original hybrid with one parent until only a small amount of the germ plasm of the other parent remains. Frequently, the effect of so small an amount of foreign germ plasm is not immediately apparent in the mongrel offspring, and must be detected by statistical or experimental means. *Uvularia* is a perennial plant, and under the best conditions each generation will take two years to grow to flowering size. In nature, some plants—particularly those of *U. perfoliata*—apparently take even longer. Experimental hybridizations and back-crosses would have involved a prohibitive amount of time. Further, since the primary question in this investigation was whether introgression is occurring in natural populations, we adopted the statistical treatment. The charts in this paper are designed to provide critical evidence for or against the presence of extensive introgression. Theoretically, continual back-crossing to the parental species would at length produce offspring in which the effect of the foreign germ plasm was so dilute that it could be detected only by the most elaborate genetic tests, if at all.

In order to study introgression, it is valuable first to become familiar with plants in which there is reason to believe it is not a factor. This led, in the present project, to the quest for "good perfoliatas" and "good grandifloras." A study of the presumably "good" specimens led to temporary criteria for these species, such as glabrousness *vs.* pubescence, relative leafiness, relative size, branching pattern, leaf shapes, etc. With the acceptance of temporary criteria, preliminary plots of the "good" populations may be drawn up. It is important that the characters used for the ordinate and the abscissa be such that for one "good" species the values will fall in one corner of the diagram, while for the other species they fall in the opposite corner. An intimate relationship between the two species would be shown by the fact that intermediates fall at some point between the two corners reserved for the "good" species, and none in the unassigned corners of the chart. In this project, following the traditional orientation of the pictorialized scatter diagram, our charts reserve the lower left corner area for one species, *U. perfoliata,* and the upper right corner for *U. grandiflora.*

The rays on the dots are so planned that one "good" species (in this case *U. perfoliata*) should be ray-less, while the other will have a complete set of full-length rays. If the variation depicted by the rays is related, we must expect that, as the dots progress from the lower left area of the chart into the upper right, the frequency and length of the rays will tend to increase correspondingly. And if that condition appears on the chart, we cannot escape the conclusion that the condition is caused by an intimate relationship between the two species.

If introgression is a factor in the populations reproduced on the charts, what evidence for this fact appears on them? The answer reveals one of the peculiar

advantages of the pictorialized scatter diagram over other methods of data presentation for the analysis of variation. On the charts, where introgression is a factor, there is a strong tendency for the sum of the measured characters to vary together. The total variation is more cohesive than the variation of the single characters making up the total. The following examples illustrate this fact.

In a population which is varying due to some environmental factor, as of a plant which grows large and lush along a stream bank and becomes gradually smaller, less branched, etc., as it grows up a slope, the variation would be something like that in fig. 7. The dots would fall on a straight line, and the rays would all increase proportionately as the dots progressed from the lower left area to the upper right.

In introgressive populations, on the other hand (fig. 8), the position of the dots forms a spindle-shaped figure of various proportions. The only areas on the chart where no dots will fall are the two unassigned corners. As the dots progress from species "A" to species "B" the sum of the rays becomes, on the average, increasingly greater, although the progressive increase of any individual ray may appear to be a random one. Note that for any given value midway on the ordinate, the values may fall along several places on the abscissa. Further, the equally variable picture presented by the rays indicates that the mongrel examples of the population express a wide recombination of characters, just as has been found in experimental crosses and back-crosses between species and races. The tendency for any one character to correlate with the sum of the other characters is therefore greater than the tendency of a single character to correlate with that of any other single character; that is, introgression (as opposed to an environmental relationship, for example) shows recombination of characters expressed as a total tendency and not as a simultaneous correlated progression of the component characters.

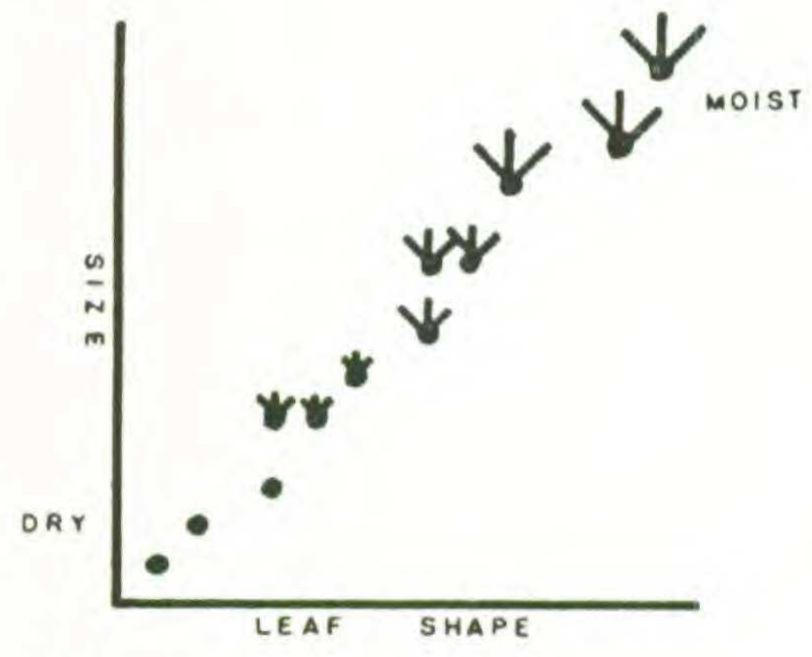

Fig. 7. A hypothetical species in which variation is due to environment. As the environment changes from moist to dry, the plant becomes increasingly small in each character. No outside genetic influence is working on the variation pattern.

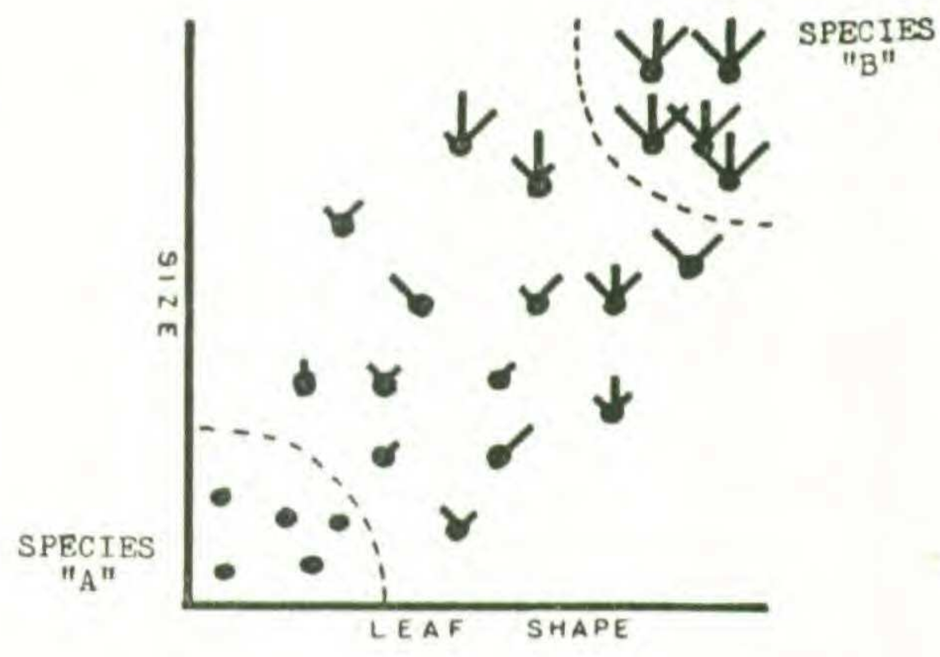

Fig. 8. Species in which introgression is causing the variation. The total ray pattern becomes greater toward the upper right-hand corner, expressing the fact that the total variation is more directional than that of any of the component characters.

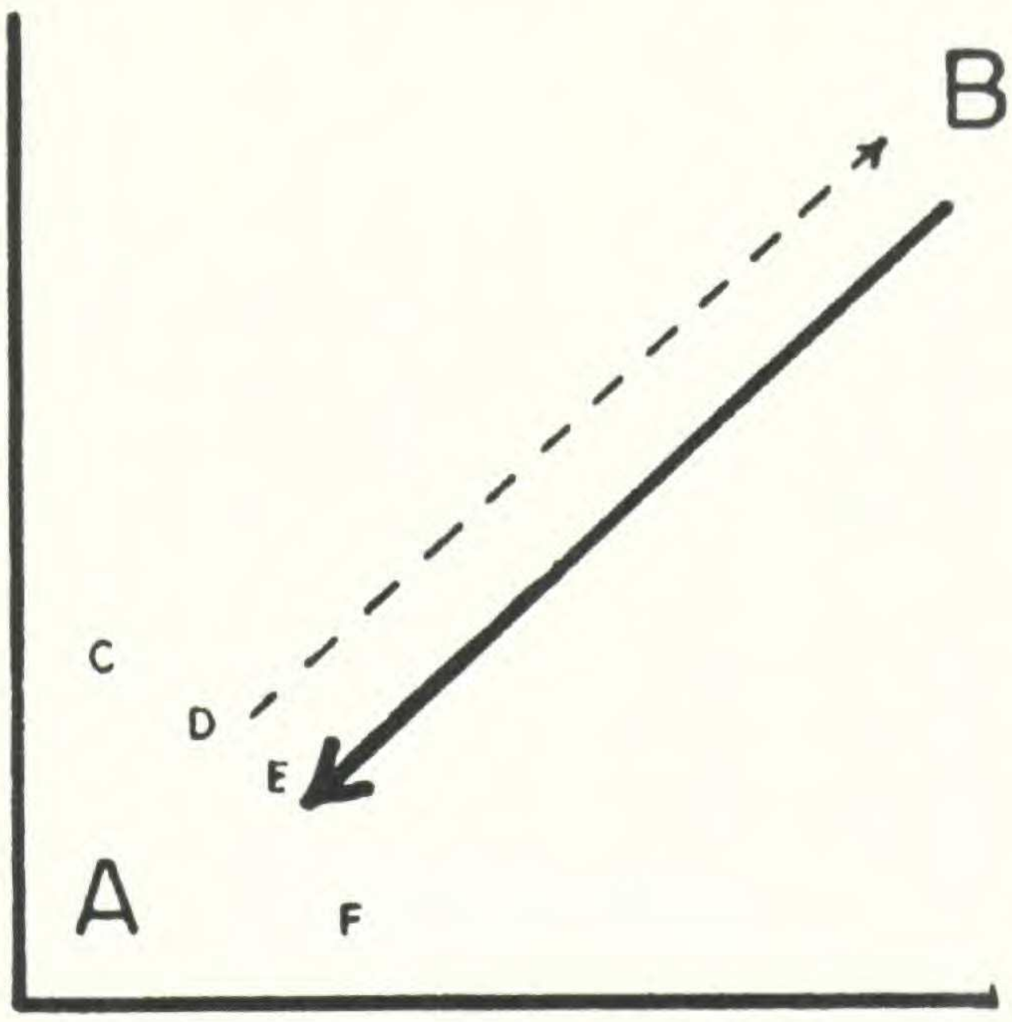

Fig. 9. See explanation below.

The ease of analyzing introgression depends upon the possible number of taxons (taxonomic entities) involved. If there are only two, the problem is simple; with three or more, it is usually very complex.

In the genus *Uvularia* there are six taxa (*U. perfoliata, U. grandiflora, U. sessilifolia, U. puberula, U. puberula nitida,* and *U. floridana*). None of these exists separated by any great distance from any one of the other perfoliate species. In some parts of the range, four taxa occur in the same geographical area. This fact raises the problem of detecting introgression between *perfoliata* and *grandiflora* without obtaining data obscured by factors originating within the taxa with which we are not presently concerned (see fig. 9, above). *Uvularia grandiflora* is markedly distinct from all the other species of *Uvularia* in a great many characters—a heavy branching pattern, multiple fruits, numerous leaves, etc. If we assign *U. grandiflora* to the upper right area of the chart, and *U. perfoliata* to the lower left area, the other four taxa might fall in a way suggested by the letters CDEF. This general picture is what we find in the present project. Actually, the four other taxa represented by CDEF, while relatively close to *U. perfoliata,* would more properly be charted in four other dimensions, although remaining in a projection of the lower left area of this chart.

In a case of this kind, we can secure valid introgression data only in the direction indicated by the solid arrow, that is, introgression of *grandiflora* into *perfoliata.* Introgression data from *perfoliata* to *grandiflora,* in the direction of the dashed arrow, would be obscured by the presence of the elements CDEF, which would come from the same direction. Because of the morphological resemblance between the various species of *Uvularia* in eastern North America, introgression of *grandiflora* into *perfoliata* is easy to detect and even, within certain limits, to

measure. Introgression of *perfoliata* into *grandiflora*, on the other hand, is so obscured by the presence of other species similar to *perfoliata* that we have no critical data for or against it.

In spite of its shortcomings, the type of statistical treatment used in this paper is superior to the standard methods of determining population averages using means, extremes, and spread, and calculating correlations from those data. The following table uses population means to describe the average plants of the fourteen field collections and three herbarium collections used in our charts. We learn little from this table except that *U. grandiflora* is generally larger than *U. perfoliata*, has a lower leaf index, more leaves, more fruit, and is pubescent as opposed to glabrous. This we already knew. If we calculated standard deviations we would discover that some populations varied more than others, and that these populations were from the area corresponding to the western boundary of *U. perfoliata*. The early statistical work in this project was done in this standard manner.

While the standard statistical procedures can and do tell us that the populations are different, and that some vary more than others, they do not tell us from whence this variation originated. The pictorialized scatter diagrams do give us this picture, subject to the restrictions outlined above.

Once the temporary criteria for "good" species are drawn up, preliminary charts may be constructed which enable us to refine our criteria to the point where the pattern of variation, if any, becomes clear. When this pattern is established, it becomes less difficult to select those characters for study which seem to express the variation pattern most clearly and to eliminate the variation which is not connected to the problem. The idea is not to construct a chart in which variation is stressed, but rather one which will express only the most essential differences between populations. If the preliminary survey of the problem indicates that introgression is not a factor in the species variation, there is no use to refine data, for no amount of data-juggling will result in a pattern which implies that introgression is a factor in the species variation.

Pictorialized scatter diagrams are just as good for demonstrating that introgression has not taken place as for showing that it has. The method was originally worked out for recording variation in fields of maize (Anderson, 1946). Begun as a purely mnemonic device, it demonstrated the importance of crosses between races of maize, and this led to its use in analyzing crosses between species of flowering plants. It is a general method of demonstrating the over-all picture in variation patterns too complex for unaided analysis. It is as useful for demonstrating the absence of character association as for its presence.

Collection	Length longest internode (mm.)	Leaf index	Total leaves	Number of fruits	Pubescence
Missouri Bot. Gard. *U. perfoliata*	95.4	.498	10.1	1.28	Absent
Missouri Bot. Gard. *U. grandiflora*	183.7	.388	15.7	1.47	Complete
Ridgewood	85.4	.506	8.9	1.06	Absent
Hawley	97.1	.461	7.4	1.00	Absent
Dyestone Creek	114.2	.560	8.2	1.00	Absent
Mountain Lake	107.1	.508	9.0	1.00	Absent
Oakwood Park	90.6	.443	8.3	1.00	Intermediate
Knoxville "A"	145.4	.431	12.4	1.05	Partial
Knoxville "B"	160.0	.346	14.2	1.06	Complete
Debbink	159.1	.352	16.3	1.12	Complete
La Barque Creek	172.0	.284	15.8	1.00	Complete
Butts	174.0	.342	15.0	1.15	Complete
Red Lake	184.1	.338	14.9	1.04	Complete
Clarksville	173.0	.306	14.5	1.08	Complete
Coxsackie	184.0	.354	15.6	1.37	Complete
Missouri Bot. Gard. "Missouri"	191.4	.372	16.5	1.50	Complete
Billington Woods	200.5	.298	16.9	2.46	Complete

Collections Giving Evidence for Charted Data

Ridgewood, N. J. (Chart 3).—Thirteen of the sixteen plants plot out as "good" *perfoliata.* There is some variation in the population, three plants having more than 9 leaves, and one with 2 fruits. While these characters tend to suggest *U. grandiflora,* there is no clear evidence that introgression has been a factor in the Ridgewood population. A 2-fruited *U. perfoliata* is atypical, but not outside the realm of normal variation for an occasional plant. If the 2-fruited plant were in an extreme position toward the *grandiflora* corner of the chart it would come under suspicion, but this is not the case.

Hawley, Pa. (Chart 4).—This is another "good" *perfoliata* population, the variation in which is mostly in the direction of larger plants with somewhat narrower leaves than is typical of *U. perfoliata.* However, since there is no concomitant increase in the ray pattern to accompany this variation, we must reject introgression in this population.

Dyestone Creek, Va. (Chart 5).—The Dyestone Creek population is composed largely of "good" *perfoliata* elements, but there is evidence that there has been some influence here from *U. grandiflora.* Of the six plants appearing highest on the internode scale, five are seen to have one or more ray fragments. On the other hand, the five plants lowest on the internode scale are devoid of rays. It then follows that the variation in this population is oriented toward *U. grandiflora* rather than simply at random. Dyestone Creek is not far from the "fringe" area in which the variation in *U. perfoliata* is so marked. There is, in fact, a suggestion in this collection of the variation pattern which will appear in the "fringe" area populations.

Mountain Lake, Va. (Chart 6).—Although west of Dyestone Creek and therefore nearer the "fringe" area, the Mountain Lake population apparently has not been influenced by introgression from *U. grandiflora.* The population contains taller plants than typical for *perfoliata,* but this may be due to environment, since there are no other connected tendencies toward *grandiflora.* There are, however, some populations in the Mountain Lake area which apparently have been influenced by introgression from *U. grandiflora.* The Mountain Lake Biological Station herbarium contains some sheets of *Uvularia,* several of which preserve what we would call "problem plants." These are occasionally identified incorrectly, but frequently they may possess some key characters of both species, and even a person familiar with the plants could conceivably be led astray. The Mountain Lake area contains plants of *U. perfoliata, U. grandiflora,* and some intermediates, as well as two other species of *Uvularia.*

The fact that our population sample does not show introgression serves to point up the fact that, even in "fringe" areas, only occasional populations display this feature. Although most of the observed intermediate populations come from "fringe" areas, it should not be implied that all fringe-area populations are intermediate.

Oakwood Park, N. Y. (Chart 7).—This population is near the western boundary of *U. perfoliata* and therefore in the "fringe" area where the greatest variation has been noted. We now can observe that this variation is due to introgressive hybridization. While the entire population consists of rather small plants, the leaves are uniformly narrower than those in Ridgewood, for example, and the picture presented by the rays shows that the *grandiflora* elements appear generally from the direction which was assigned to that species. The dots in the lower left area of the chart are generally without rays. Those in the upper right portion are all partially rayed. This is the population in which we found the intermediate pubescence. The rays are not distributed at random on the chart, but instead follow a path from the upper right, or *U. grandiflora* position. Therefore the population is intermediate because of introgressive hybridization.

Knoxville, Tenn., Collection "A" (Chart 8).—This population is really intermediate. It is located near the center of the chart, midway between *U. perfoliata* and *U. grandiflora.* In addition, the rays are more frequent and longer in the upper right portion of the plot. The plant in the lower left has a long ray to the right, indicating pubescence. While there is no doubt that this is a *grandiflora*-type pubescence, it only appeared on a portion of a single leaf and the rest of the plant was glabrous. Had we called the plant glabrous, the dot would have appeared with only a fragment of a ray off to the left, indicating a slight leafiness.

The population, essentially *U. perfoliata,* is growing in a moist area. This is not usually true for "good perfoliatas." The fact that the plants do well in this environment may be attributed to the adaptability they have acquired as a result of the introgression from *grandiflora.*

Knoxville, Tenn., Collection "B" (Chart 9).—This is essentially a *U. grandiflora* population. The picture presented by the rays presents a generally random variation. The plants average smaller than "good" populations of *U. grandiflora* should, but there is no evidence to indicate that size is not an environmental condition, or, if the result of introgression, from which small *Uvularia* the condition came.

Debbink, Wisc. (Chart 10).—These plants, like the preceding ones, are small for *U. grandiflora.* There is a slight tendency for the rays to be longer in the upper right portion of the chart than in the lower left. However, again we have no way of determining the origin of the non-*grandiflora* element which this tendency reflects, if there is actually such an element in the population.

La Barque Creek, Mo. (Chart 11).—Although variable, the variation is at random in this charted population.

Butts, Mo. (Chart 12).—The position and totality of the rays on this chart offer a faint suggestion of introgression from some non-*grandiflora* source.

Red Lake, Minn. (Chart 13).—The variation in this population with respect to *perfoliata-grandiflora* introgression is at random. Though outside the scope of this investigation, the Red Lake collection suggests strongly an introgression from *U. sessilifolia.*[3] This is reflected in the chart by the rather amorphous variation of the plots. There is no tendency toward *U. perfoliata,* in spite of the low degree of cohesiveness. This fact tends to indicate that the design of the charts has met with the demand that it reflect the *grandiflora-perfoliata* tendency without influence from other variation factors.

Clarksville, Mo. (Chart 14).—In this collection we see again a faint suggestion of introgression from a non-*grandiflora* element. There is no indication that this element is *U. perfoliata.*

Coxsackie, N. Y. (Chart 15).—The Coxsackie collection is from an area where the two species grow near to each other. While the population as a whole is quite *grandiflora*-like, there is a strong suggestion of introgression with *U. perfoliata.* This may indeed be true, but the design of the chart is such that introgression from *U. perfoliata* into *U. grandiflora* is not provable. However, since we have striven to eliminate much of the variation from directions other than that between *perfoliata* and *grandiflora* from the chart, we can state that the Coxsackie population probably represents introgression from *perfoliata* into *grandiflora.*

Missouri (Chart 16).—This synthetic population sample from herbarium sheets in the Missouri Botanical Garden reflects the general condition found in the individual Missouri collections. As a whole, these plants represent a "good" *grandiflora.* There is a slight tendency for plants with complete ray systems to be higher and farther right on the chart than those with incomplete ones, but there is no proof that this variation is from *U. perfoliata.*

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[3] This suggestion is expressed by the following facts: (1) the presence of some sessile leaves on the upper portions of occasional plants; (2) the 90° angle of the primary branch, as in *U. sessilifolia,* rather than one of about 60°, as in *U. grandiflora*; and (3) the gross appearance of the plant which is similar to that of the sessile-leaved species of *Uvularia.*

Billington Woods, Mich. (Chart 17).—This is, on the whole, an excellent population of *U. grandiflora.* Of the eighteen plants, fourteen (78 per cent) have 3 rays, and of these fourteen plants (67 per cent of the total) have complete ray systems. The four plants with only two rays appear at random on the chart.

INTERPRETATION OF THE VARIATION IN THE PERFOLIATE UVULARIAS

As has previously been discussed, the only clear evidence for or against introgression in the perfoliate species of *Uvularia* is from *U. grandiflora* into *U. perfoliata.* The *grandiflora* populations are often quite variable, but we cannot prove that this is due to introgression from *perfoliata.* On the contrary, we have reason, from the charted data, to believe that in many cases this is not true. The Coxsackie *grandiflora* population appears to have been influenced by introgression from *perfoliata,* and the chart indicates that this is probable, but other non-perfoliate species might be involved.

One of the most significant facts to be gleaned from the charted data is the relative rarity of introgression as a factor in the perfoliate Uvularias. We can reason that if these species hybridized easily in nature, large numbers of hybrid populations would occur throughout the area of mutual distribution. This is not so. Generally, throughout the area of overlapping distributions, each species population is distinct. Most of our typical specimens of *U. perfoliata* come from areas where *U. grandiflora* is not far away.

Once a hybrid does occur in nature, however, the way is clear for introgression to proceed. *Uvularia* is a perennial plant. It is not necessary for it to set seed each year in order to survive. Propagation is largely vegetative. The F_1 plant, then, once it occurs, can exist without genetic change (unless by mutation) for a long period of time. Since we have reasoned that these F_1 plants must be rare, it follows that at such a time as cross-fertilization occurs again in that plant, it must be between the F_1 and one or the other parent species, most likely the one closest by; in other words, a back-cross. This back-cross will resemble the parent with which the F_1 was hybridized, except that some of the characteristics of the other species may remain. In time this back-cross generation may again hybridize with the primary parent species. The cross would logically occur thus, since we have postulated that the F_1 hybridized with the parent species most adjacent to it, and the back-cross would behave similarly. Thus a second back-cross generation is formed which contains no less than seven-eighths of the characteristics of the primary parent species and no more than one-eighth of those of the secondary parent species. Genetically, it is possible to reconstitute the original species even in the first back-cross. In nature, those back-crosses with the fewest elements of the foreign species are those most likely to survive under natural conditions (Anderson, 1948). As a result of crossing between the two species, we are most likely to find back-crosses closely resembling the original primary parent species but slightly variable in the direction of the non-recurrent parent. The results of such hybridizations and back-crosses is that a genus such as *Uvularia* could persist unchanged for long periods of time, hundreds or even thousands of years.

The question then arises: Why should this condition not be prevalent throughout the areas shared in common by the two species, rather than primarily at the edge of the range of *U. perfoliata*? Away from the "fringe" areas of the specific distributions the environment is relatively uniform, and the potential parents are occupying ecological niches for which they are suited. Occasional crosses present no particular advantage to the hybrid, or they may even present something of a disadvantage with respect to the niches for which the parents have become adapted. After a time the hybrids would tend to disappear. This may have been the case with *U. flava,* the species which Smith established at the same time that he established *U. grandiflora. U. flava* appeared to be essentially like *U. perfoliata,* but it possessed flower characteristics like those of *U. grandiflora.* From the descriptions it appears that *U. flava,* considered rare and found "from New Jersey to Virginia," was probably an introgressive hybrid, or perhaps even an F_1, which did not add any particular advantage to the *perfoliata* element. *U. flava* apparently disappeared gradually, for the manuals of the day reflect increasing uncertainty about it until it finally was dropped into synonymy with *U. perfoliata* and was removed entirely from the literature. We have found no records of *U. flava* collections for more than sixty years, nor do we know of any botanists who claim to have seen this form in recent years.

What then is the significance of introgression as a factor in the perfoliate species of *Uvularia?* Introgression provides a reserve of adaptability on which the plant can draw, under conditions differing from those for which the parent species have become adapted. If conditions change, or if the plant migrates away from the area in which the parent species are successful, this reserve is available, with the consequence that the introgressive hybrid is more likely to be successful. The successful form differs, albeit slightly, from the parent species. Projecting this into the future, the introgressive hybrid represents a possible step in the differentiation of another kind of plant. It is the potential ancestor of a new species, which can survive and evolve in environments where the parent species would be less likely to do so. It is free to evolve to occupy a different niche than those which its relatives occupy.

The study of introgression properly belongs in the field of micro-evolution, which sheds light on a portion of the still greater field of evolution itself.

Summary

Over most of their ranges, two species of *Uvularia, U. perfoliata* and *U. grandiflora,* are good and distinct species. There are some populations, however, which are quite variable and possess characters intermediate between the two species. These populations are most frequent along a line roughly corresponding to the western border of the distribution of *U. perfoliata,* and this species exhibits the greatest portion of the observed variation.

It was suspected that this variation was due to introgressive hybridization. To determine whether or not this were true, extensive measurements of both the good

species and the variants were taken. Introgression is generally so subtle that special methods for its detection must be employed. These methods may be either statistical or experimental. Since *Uvularia* is a perennial, and the experimental data would involve a prohibitively long investigation, the statistical method was employed. Because of the presence of other species quite similar to *U. perfoliata,* it is shown that introgression from *perfoliata* into *grandiflora* would not be readily demonstrable, although the reverse introgression *(grandiflora* into *perfoliata)* could readily be demonstrated if it does indeed occur.

The statistical data were reduced to charts designed primarily to reveal the influence of *grandiflora* on *perfoliata,* if such influence existed. The charts demonstrate introgression from *grandiflora* into *perfoliata* in some populations.

These introgressive populations were most abundant along the western border of the distribution of *U. perfoliata,* rather than throughout its range. The introgressive populations have a survival value due to greater adaptability which enables them to be successful outside the ecological niches occupied by the parent species. When they are found in new ecological niches they will frequently persist. They may represent the beginnings of potential new varieties, which might eventually lead to new species.

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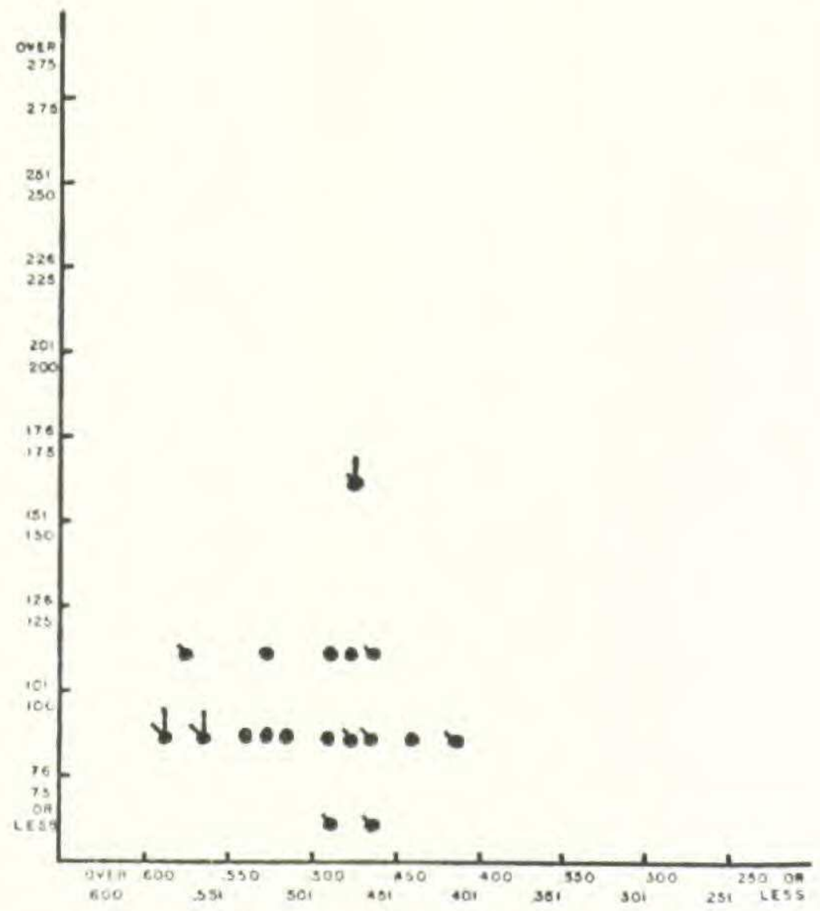
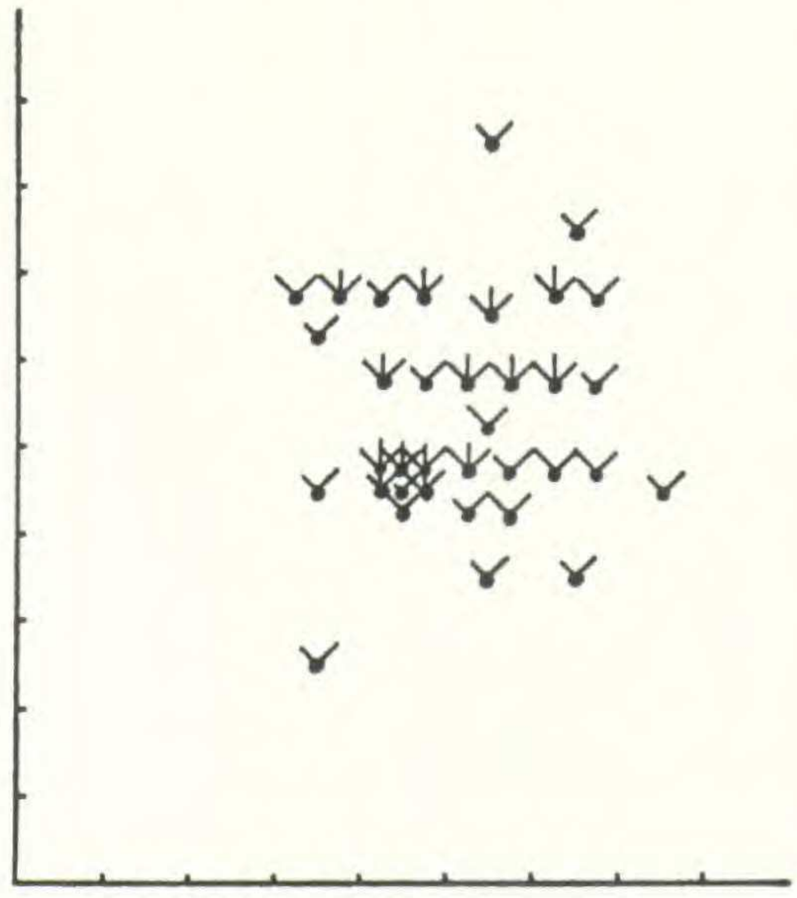


CHART 1 MBG.
PERFOLIATA



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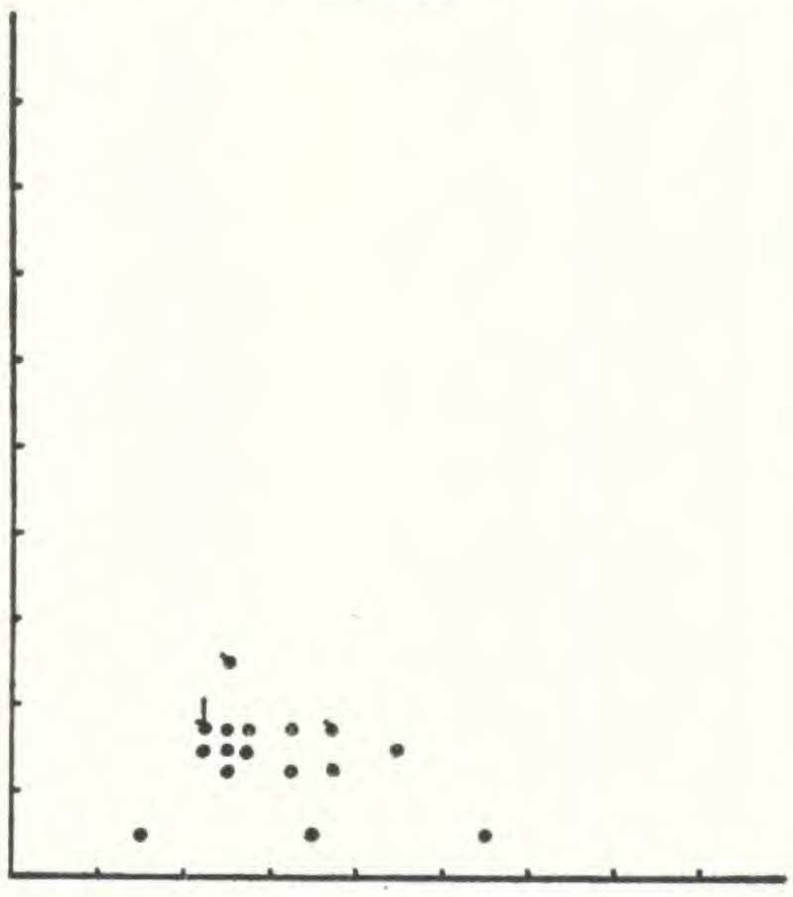
GRANDIFLORA



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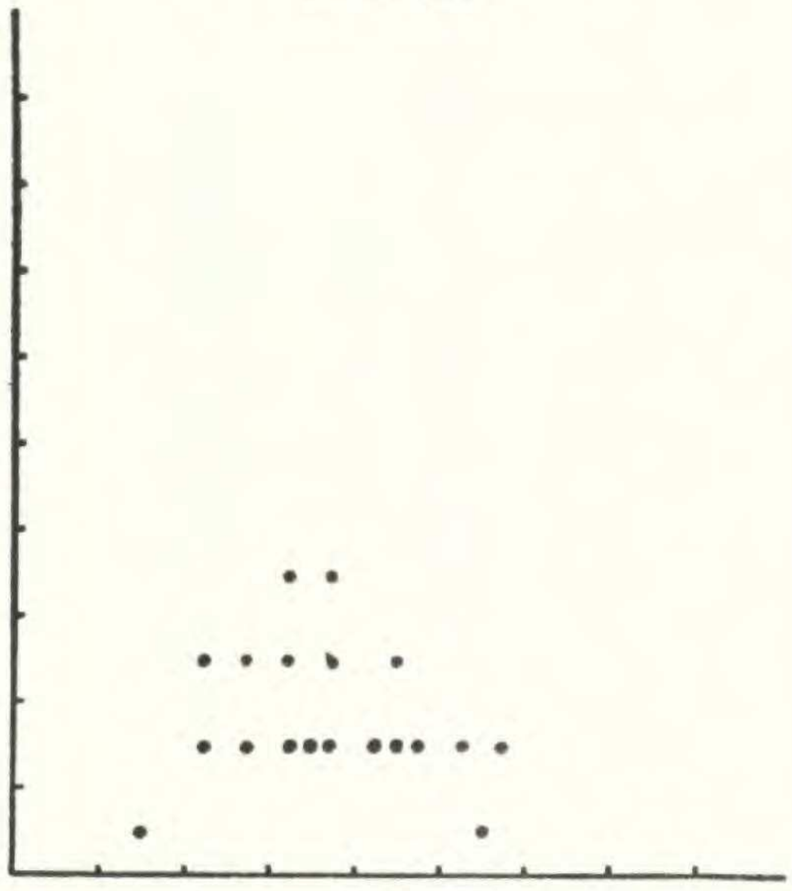

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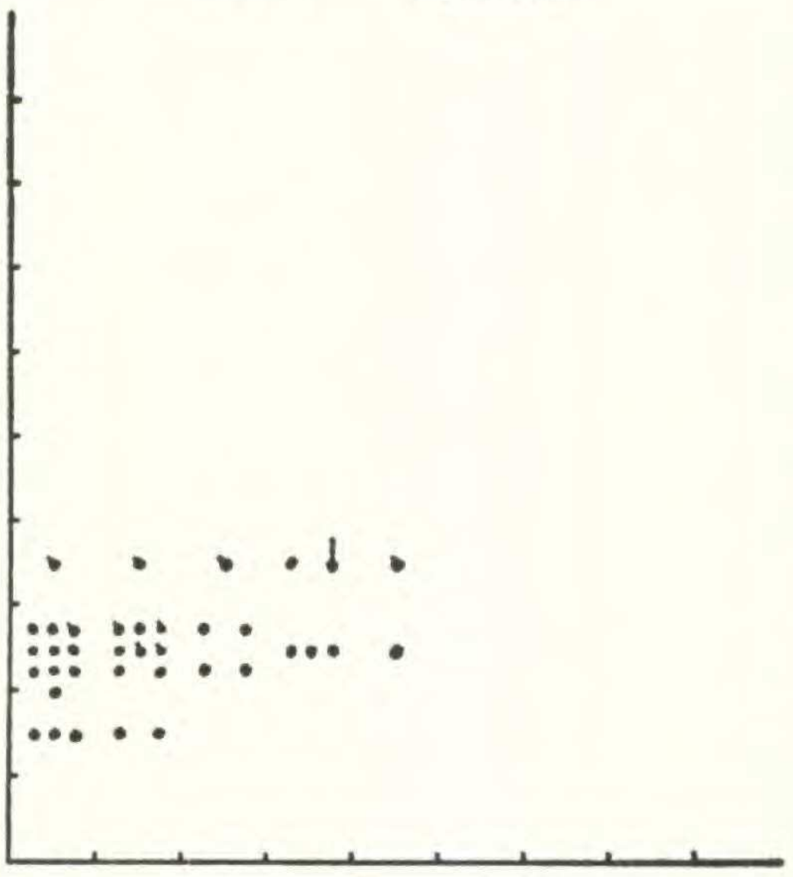

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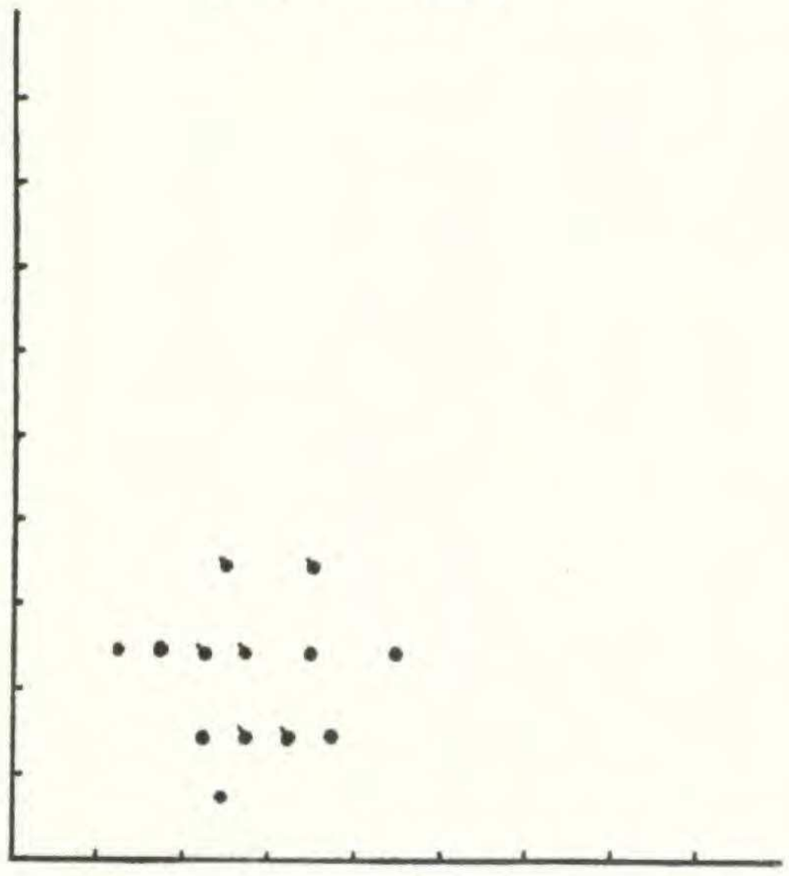

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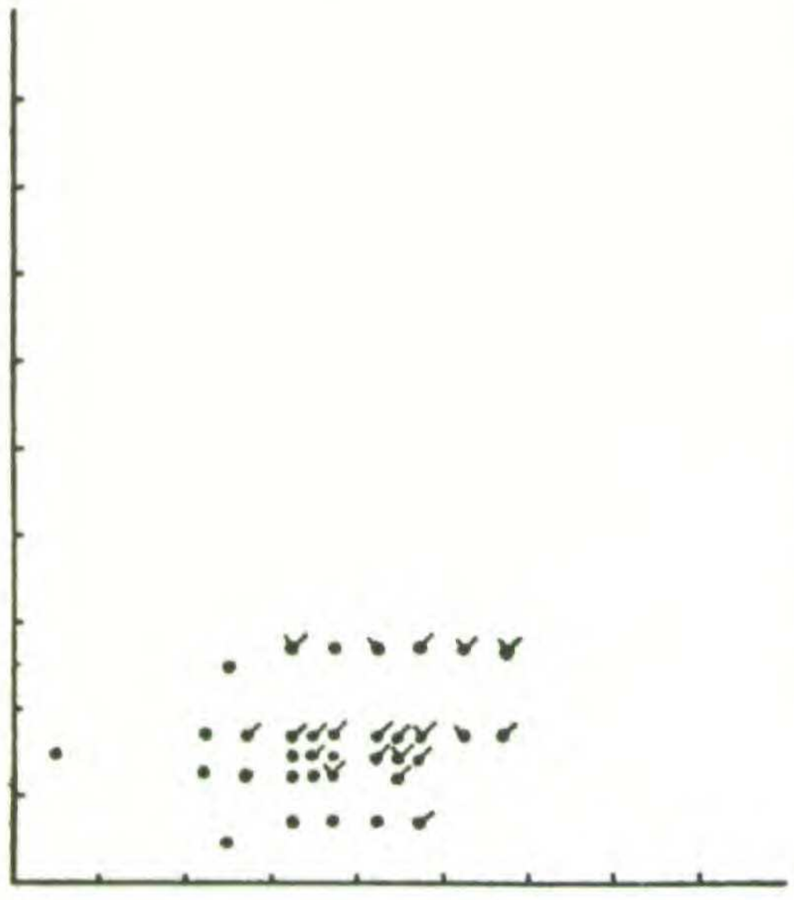

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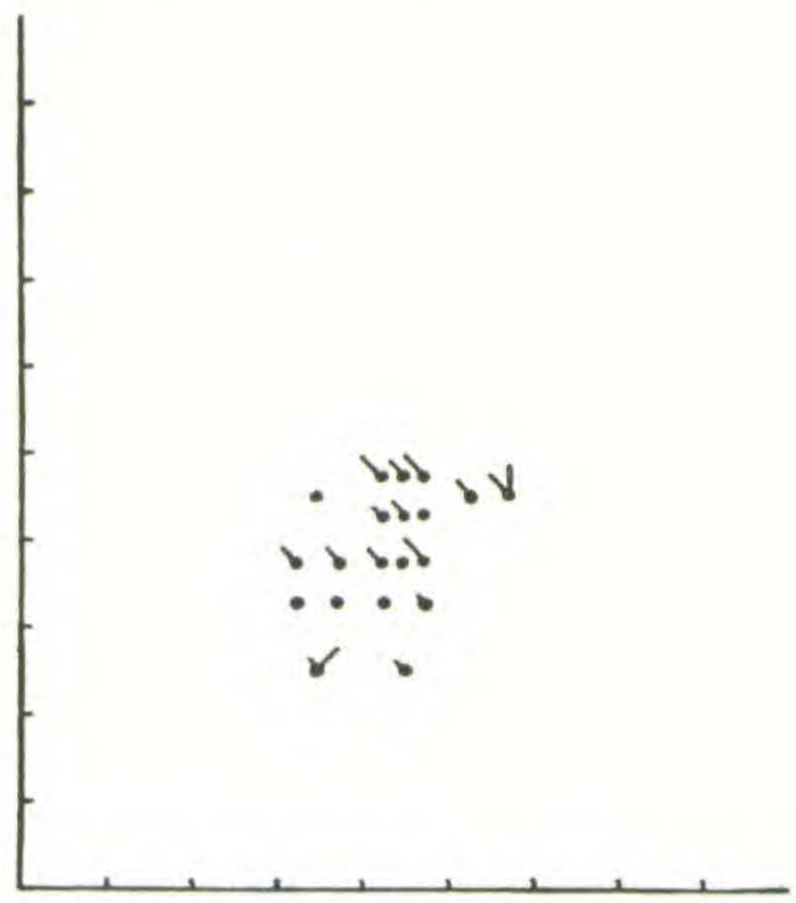

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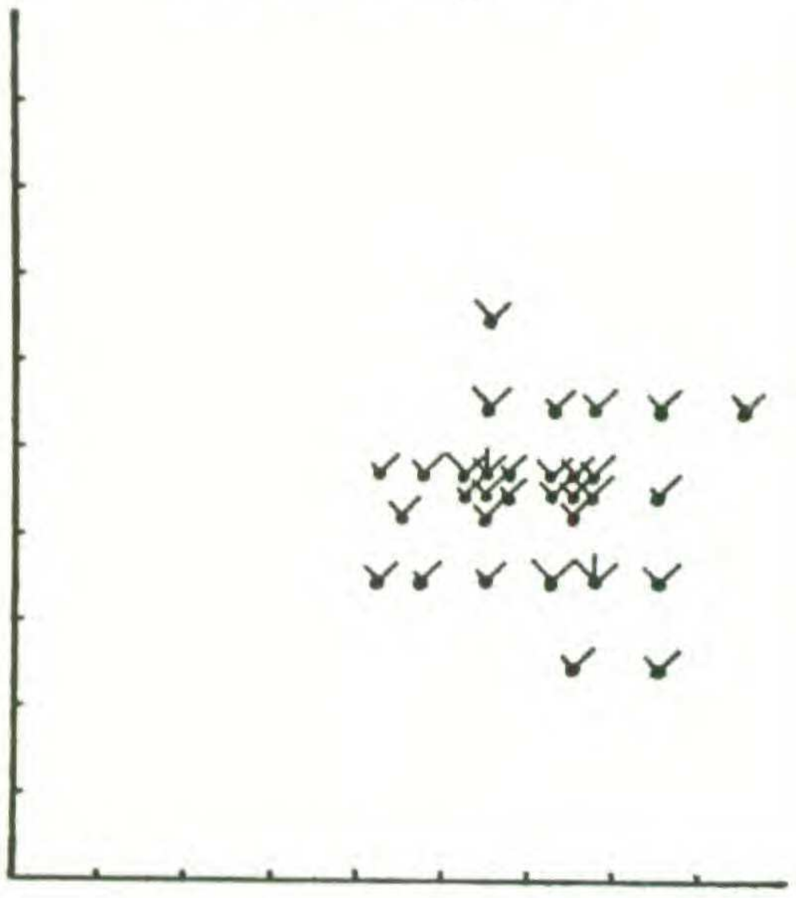
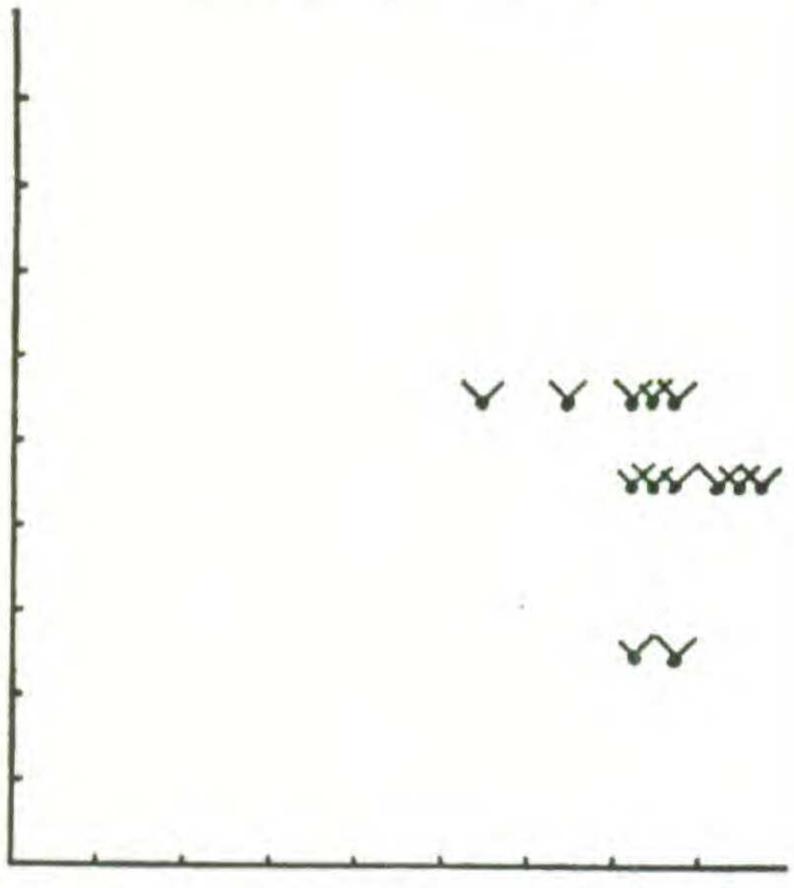


CHART 9 KNOXVILLE "B"

CHART 10 DEBBINK



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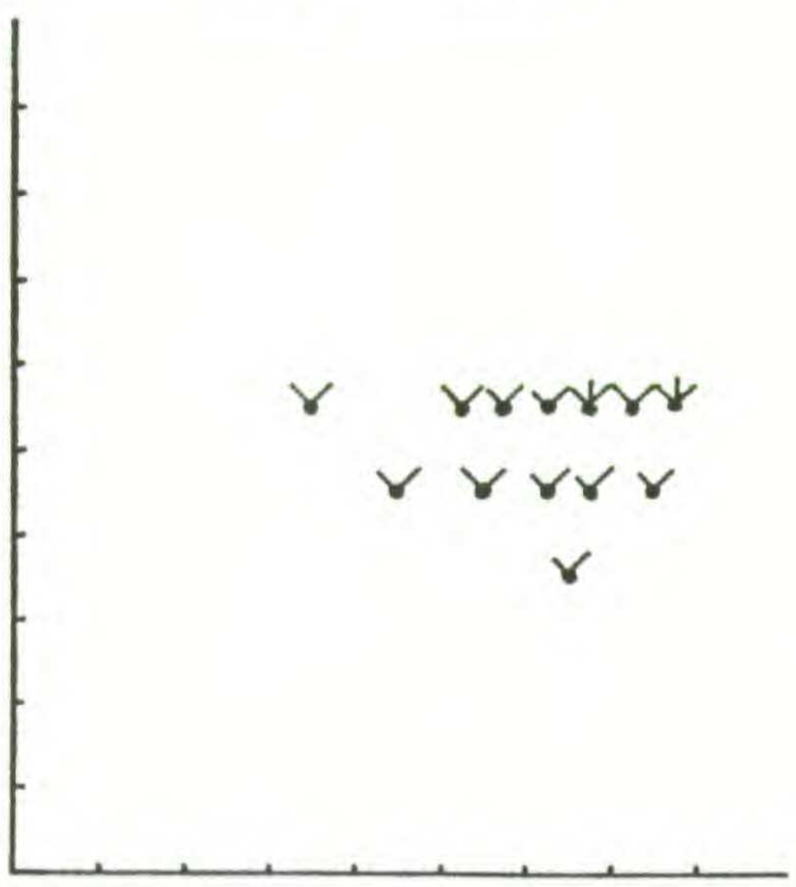

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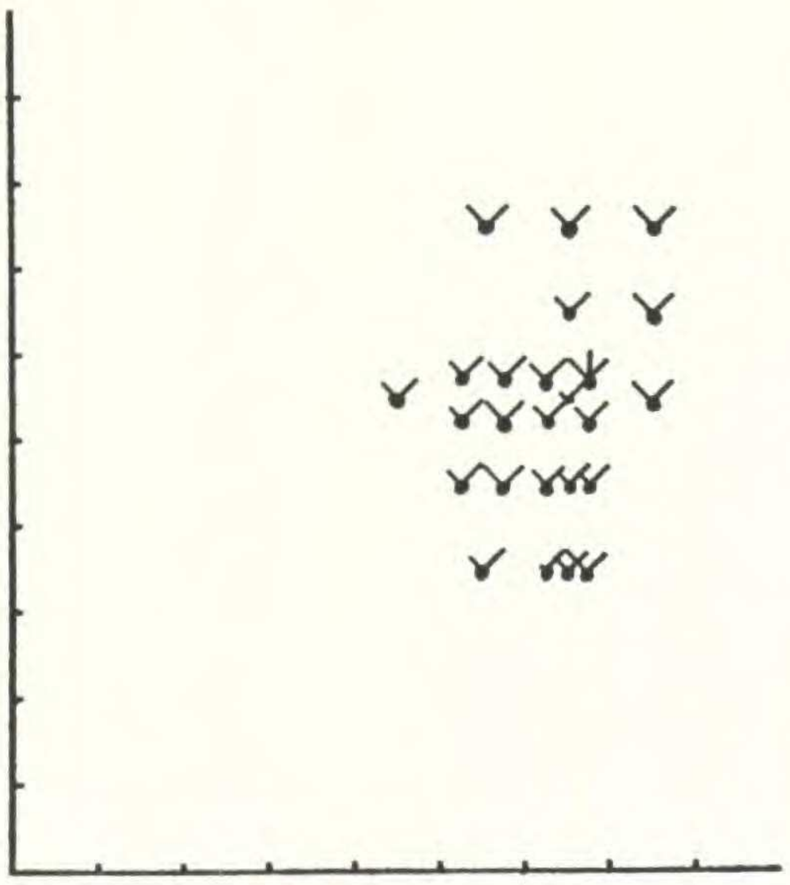

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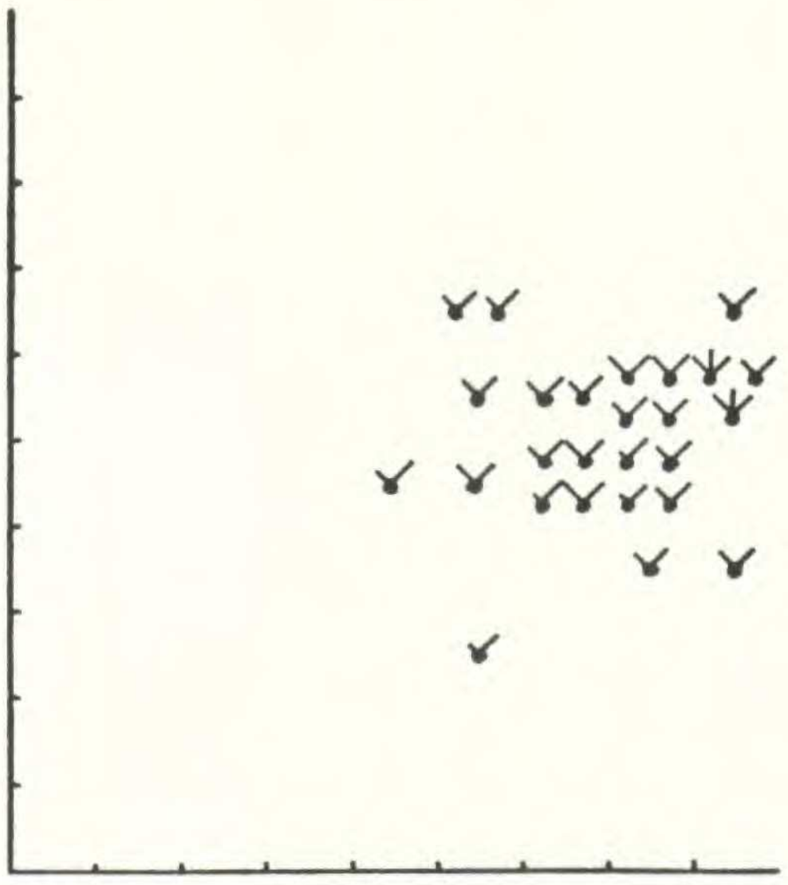

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CHART 15 COXSACKIE

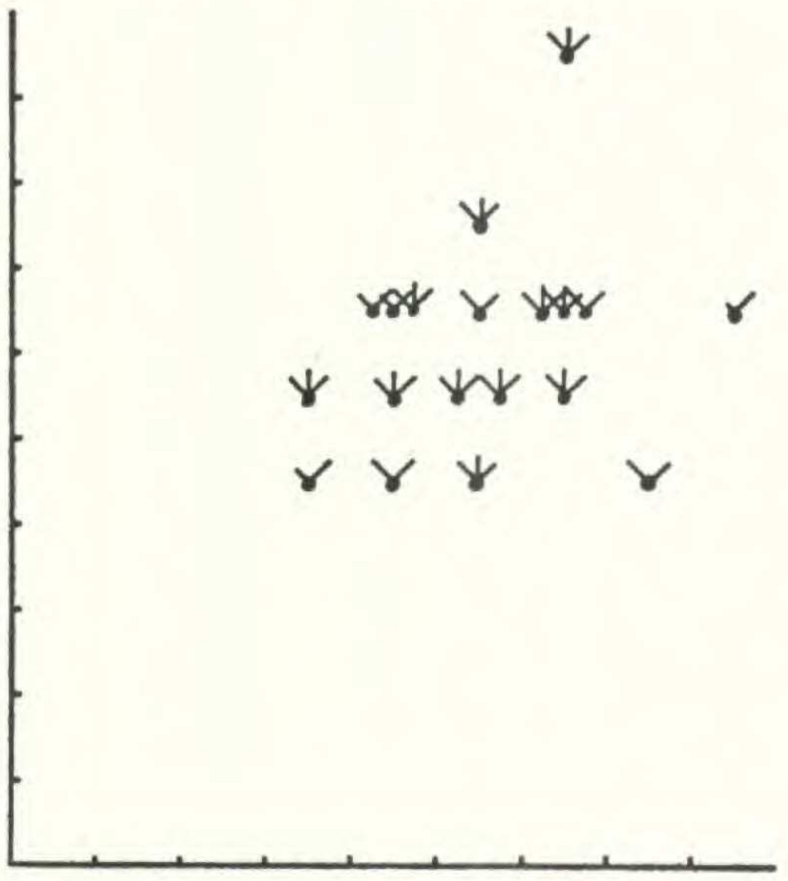

CHART 16 M.B.G.
MISSOURI

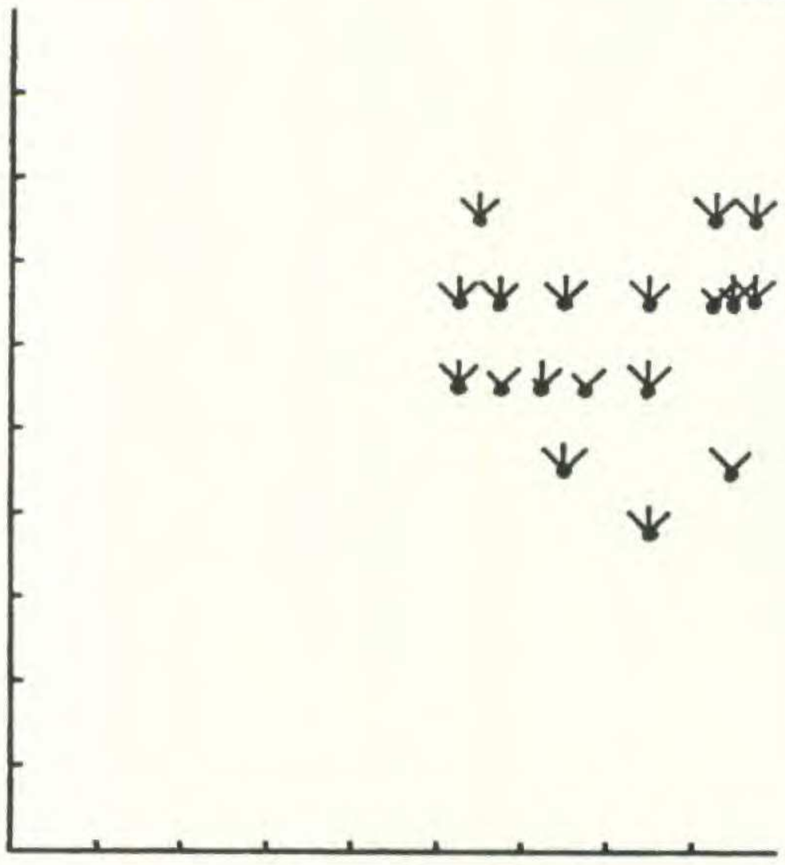

CHART 17 BILLINGTON